YEARBOOK

OF AGRICULTURE

UNITED STATES DEPARTMENT OF AGRICULTURE

Organization

of the United States Department of Agriculture

CORRECTED TO JULY 1, 1937

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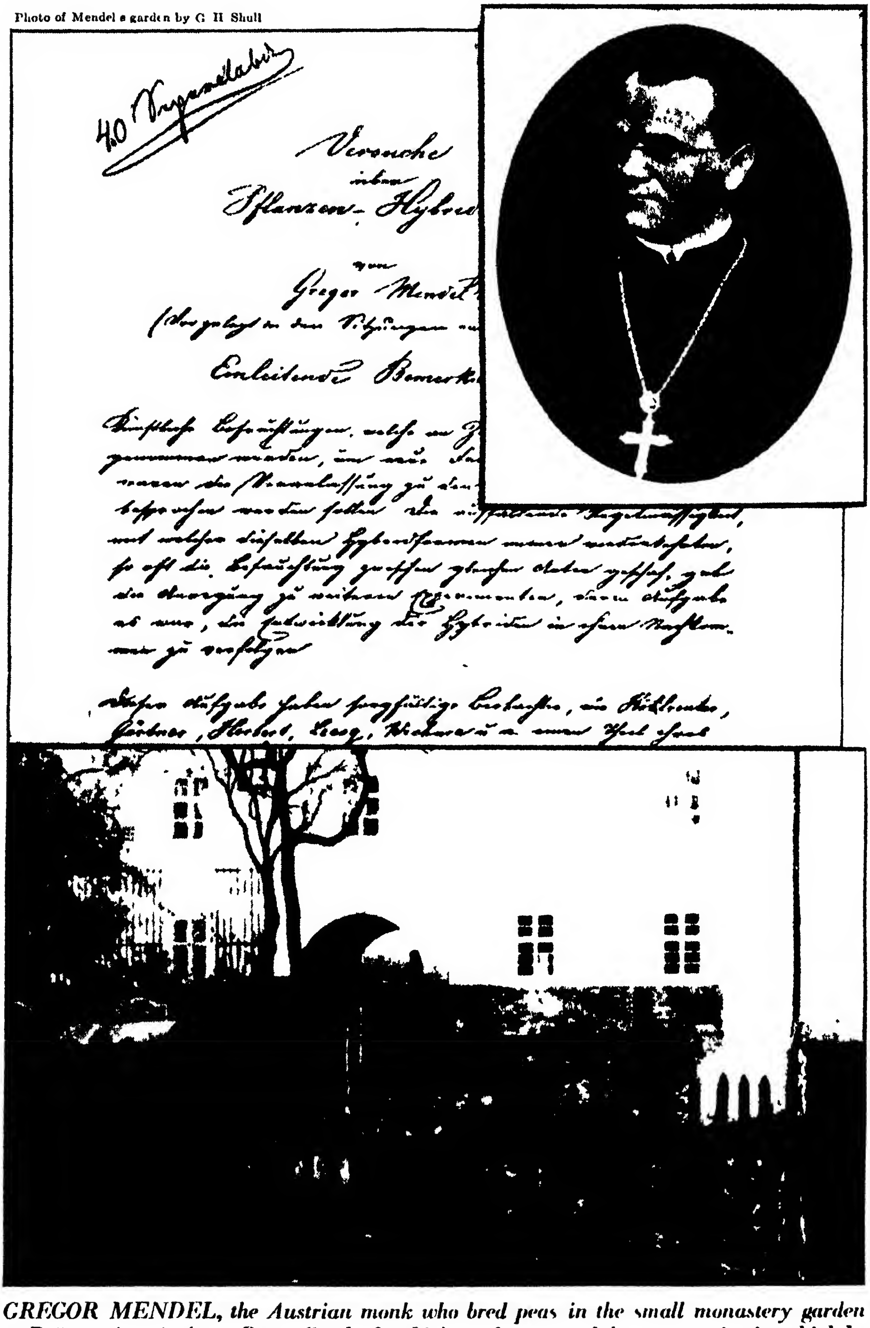
Contents

LIMITATIONS *of space made it necessary to omit from this volume some of the ma erial prepared as a result of the survey of plant and animal improvement. Two complete articles were omitted—one on the Improvement of Subtropical Fruits Other than Citrus, by Hamilton P. Traub and T. Ralph Robinson and one on the chromosomal basis of heredity (Studies in the Behavior of Chromosomes) by A. F. Blakeslee, consulting member of the Secretary's Committee on Genetics. Both of these articles, however, will be published in the 1937 Yearbook Separates, obtainable from the Superintendent of Documents, Washington, D. C., at a nominal cost. In order to keep the record complete and unified, the summaries of the articles have been retained in the introductory chapter beginning on page 119. The remaining omitted material consists of the bibliographies on flower breeding and on forest-tree breeding, which include a large number of references, and which will also be published with the text of the articles in the Yearbook Separates; and a few pages of miscellaneous agricultural statistics. The latter are included in substance in the volume entitled Agricultural Statistics, 1937, obtainable from the Superintendent of Documents. A notice of the fact that Agricultural Statistics would hereafter be published as a separate volume appeared in the foreword to the 1936 Yearbook.*

Photo of Mendel's garden by G. H. Shull



GREGOR MENDEL, the Austrian monk who bred peas in the small monastery garden at Brünn, Austria (now Brno, Czechoslovakia), and a page of the manuscript in which he announced, in 1868, the fundamental laws of heredity he had discovered. Mendel's researches attracted no attention until the rediscovery of his work in 1900. Then Mendelism became the foundation for modern plant and animal breeding.

THE YEAR IN AGRICULTURE

REPORT OF THE SECRETARY OF AGRICULTURE TO THE PRESIDENT OF THE UNITED STATES, WASHINGTON, NOVEMBER 10, 1936

PROGRESS OF FARM RECOVERY

FOUR years ago American agriculture was in the depths of depression. Though farm commodity prices had dropped to nearly 50 percent below the pre-war average, the prices of the goods and services that farmers usually buy were at or above the pre-war level. This disparity was a cause of widespread agricultural ruin. Farm bankruptcies were at record heights, dispossessed farmers joined the urban unemployed, and farmers still struggling could not make ends meet. There was a tremendous surplus of farm products; yet consumers were suffering scarcity. Falling farm prices did not help them much, because their incomes were falling too as a result of declining trade and employment. The whole economic system was out of balance.

Since then conditions have changed for the better. The improvement has come about in the manner envisioned in 1933—through agricultural-price recovery with resulting increased demand for city goods. Net farm income this year will be three times that in 1933. All groups of farmers and all agricultural regions have participated in the recovery, though not to the same degree. There is still distress in some regions, as a result of drought in 1934 and again this year. On the whole, however, agriculture is out of the red and making progress toward financial rehabilitation.

This improvement has not been accomplished at the expense of other economic groups. On the contrary, it has promoted their welfare. Consumer buying power has risen with farm incomes, and the average employed wage earner can buy more food today than he could at the peak of urban prosperity in 1929. Food prices are still 15 to 20 percent below the predepression level. In spite of two great droughts in 3 years the total food supply for the current marketing season will be within 1 or 2 percent of what it was in 1935–36. Meat production is below normal requirements; but the output of some other products has increased, and exports are relatively low. Hence the national average per-capita consumption of foods has shown little change. Industrial production is 80 percent above the low point of 1932. In short, the economic system has moved toward balance, with larger incomes in both town and country, and with profits replacing deficits in both farm and city balance sheets.

Farm recovery began in 1933 promptly after the adoption of a national farm-readjustment program, accompanied by revaluation of the dollar. As the farm income rose, farmers started clearing off their debts and taxes. They recommenced buying industrial goods. Recovery went on at a faster pace in 1934, 1935, and 1936, despite the handicap of drought. Between 1932 and the end of 1934 shipments of industrial goods to agricultural areas increased nearly 43 percent, and shipment of goods used in farm production increased 75 percent. New-car registrations in agricultural States in the first half of 1935 were 147 percent larger than in the first half of 1933. Farmers were not monopolizing the benefits of farm recovery but were diffusing it throughout the country and putting life blood into business. What nonfarmers had contributed in processing taxes and benefit payments they got back with interest. Reciprocally the revival of urban trade benefited agriculture, and the whole economic picture brightened.

The Production-Control Programs

In the early stages of the farm recovery, the production of farm commodities had to be restricted so as to reduce the surpluses that were not moving into foreign markets. When drought in 1934 and again this year reduced production too drastically, some people questioned the logic of crop adjustment. Scarcity, however, was never intended and never approached. This country's farm productivity is so tremendous that recovery from drought comes quickly. Full use of the available acreage normally means surpluses. Agriculture produced as usual in the first years of the depression, while urban industry reduced its output by nearly 50 percent.

In bringing their production more nearly in line with demand, farmers were simply copying the behavior of other groups when faced with overproduction and declining markets; with the important difference, however, that only export surpluses came within the farm-reduction program. As soon as the demand improved, farmers increased their acreage and livestock breeding. Though drought in 1934 and 1936 kept the production from rising proportionately, it will rise eventually. Both the farmers and the present National Government aim at adequate production for domestic requirements, plus whatever additional supply can be sold profitably abroad.

Undoubtedly, most Americans want to maintain our agriculture on a proprietary, landowning, family basis. Certainly this Administration does. It is not desirable to have either a peasant agriculture manned by tenants and laborers, or a collective agriculture run by the central Government. This idea involves certain responsibilities. Farmers must be permitted to earn a profit, a margin of income over expenditures; otherwise the family farm becomes bankrupt, and either tenancy or Government farming supervenes.

But if agriculture is to be profitable, it must have prices sufficient on an average and in the long run to exceed its fixed charges and expenses of production; and this is impossible when supplies greatly exceed the effective demand. Those who object to the rational adjustment of the farm output to the farm demand practically take the position that farmers should produce, without regard for the reward obtainable, as long as anyone needs their crops. Needless to

say, production on that basis cannot continue in any business. Profitable farming, in short, means farming adjusted to the available market. If want continues after that has been accomplished, the remedy is to create more buying power, rather than to compel farmers to produce indefinitely at a loss.

Comparison With Industrial Production

Farmers cannot be charged with having promoted scarcity when they readjusted their production for export more nearly in line with the available market. Index numbers of production and prices have been computed in this Department, with the 5 years 1925 to 1929 taken as 100. Farm production was 100 in 1930 and 106 in 1931, from which point it declined moderately to 90 in 1934 and 1935. Industrial production fell year by year after 1929 until it reached a low point of 56 in 1932. Thereafter it recovered gradually until in 1935 the index stood at 82, as compared with the farm production index of 90. It should be borne in mind that the industrial index includes the output of food manufacturers, an item which, of course, reflects farm production. Were this item excluded from the industrial index, the contrast between farm and factory production would be still more striking. Farm production remained high and farm prices relatively low until farm adjustment got under way. Industrial production and prices showed the reverse relationship.

Moreover, the farm situation in 1933 was such that reduced production would have come about eventually in any case, with or without Federal assistance. That is the typical end-product of low prices. Usually, reduced production results from drastic competition and the elimination of the weaker producers. Concerted action after 1933 enabled the vast majority to survive. But this procedure did not reduce production more than it would have been reduced eventually by the other process, and it prevented deterioration of the agricultural plant through farm abandonment.

Looking back over the last 4 years, we can see that despite the droughts we have advanced toward balanced abundance. Four years ago our factories were producing below and our farms above consumer requirements, with both branches of production losing heavily. Today we have a forward movement in both town and country. Farm recovery has reanimated urban life without hurting any group. The disparity between urban and rural production has been substantially removed; likewise the disparity between farm and nonfarm prices. That the results have been beneficial everyone can testify from his own experience. Our higher national income, our increased employment, and the increase that has taken place in the money value of both agricultural and industrial assets show that recovery has been general.

FARM INCOME AND BUYING POWER

This Department makes available two series of farm-income statistics. One series records current receipts from sales plus A. A. A. payments, and the other shows the estimated gross income from the production. Farmers' receipts from sales plus A. A. A. payments in 1936 will probably reach $7,850,000,000, or about 11 percent more than

the corresponding receipts in 1935. This figure is 81 percent more than the cash farm income of 1932 and only 25 percent less than that of 1929. Table 1 shows the decline that took place from 1929 to 1932 and the subsequent steady recovery:

TABLE I.—*Changes in income from 1929 to 1936–37*

Calendar year	Cash income from marketings	Crop year	Gross income[1]
1929	$10,479,000,000	1929-30	$11,941,000,000
1930	8,451,000,000	1930-31	9,454,000,000
1931	5,899,000,000	1931-32	6,968,000,000
1932	4,328,000,000	1932-33	5,337,000,000
1933	5,117,000,000	1933-34	6,406,000,000
1934	6,387,000,000	1934-35	7,276,000,000
1935	7,090,000,000	1935-36	8,508,000,000
1936[2]	7,850,000,000	1936-37	9,200,000,000

[1] Includes cash returns from calendar-year marketings of livestock, and from crop-year marketings of crops plus the farm value of production retained for use in the farm home. A. A. A benefit payments included in gross-income estimates as well as in the annual cash income service.
[2] Preliminary.

It will not be possible to indicate in detail the gross income from the farm production in 1936 until well along in 1937, when the marketings will be more nearly completed. It probably will approach $9,200,000,000, as compared with $8,508,000,000 from the production of 1935. It represents a total advance of about $3,900,000,000 or 72 percent, from the low point of 1932, but it is about $3,000,000,000, or 23 percent, below the figure for 1929. Gross income in that year was 17 percent higher than in 1934–35 and 59 percent higher than in 1932–33. It was 71 percent of the 1929–30 total.

Net income remaining to farmers increased after 1933 proportionately more than the gross income because farm-commodity prices rose more than production expenses and other charges. After paying current production expenses, allowing for the depreciation of buildings and equipment and deducting rent, interest, taxes, and the wages of hired labor, the income available to farm operators for their labor, capital, and management from the production of 1935 was $4,538,000,000. This may be compared with $3,467,000,000 in 1934 and $1,492,000,000 in 1932. Whereas the increase in the gross income from 1934 to 1935 was only 17 percent, the increase in the income available to farm operators was 31 percent. It will be noticed that it was more than three times as large as in 1932. Moreover, much of the expenditures for production items in 1935 went for machinery, buildings, and repairs, which are in the nature of permanent improvements. Farmers' expenditures for capital items in 1935 approximately equaled the estimated depreciation of their buildings and equipment, for the first time since 1930.

EXCHANGE VALUE OF FARM PRODUCTS

Another index of the farm position is the ratio between prices received and prices paid by farmers. Farm commodity prices have risen more since 1933 than the prices of nonfarm goods and services. Previously the trend had been in the opposite direction. In March

1933, with agricultural prices only 55 percent of the pre-war average, nonagricultural prices were still at 100 percent of the pre-war level. Farm products in 1935 averaged 108 percent of pre-war prices, while nonagricultural prices had risen to 125 percent. Farm prices had gained on nonfarm prices, but had not attained pre-war parity. This ratio indicates the exchange value of farm commodities or their unit purchasing power. The index of farm-commodity purchasing power was 55 percent of pre-war in March 1933, 73 percent for the year 1934, and 86 percent for the year 1935. By August 1936 it had climbed to 98 percent.

The purchasing power of farm commodities is not identical with the purchasing power of the farmer. It indicates what a given quantity of farm products will buy, but not what the total volume will command. A closer estimate of the farmer's purchasing power can be derived from the ratio between the cash farm income and the prices that farmers have to pay for goods and services. With prices paid by farmers in 1936 equal to 80 percent of what they paid in 1929, the 1936 cash income of $7,850,000,000 is equivalent to $9,800,000,000 in terms of 1929 nonfarm prices. Otherwise stated, the purchasing power of the cash farm income in 1936 will be only 7 percent less than that of 1929. As compared with the purchasing power of the cash farm income in 1932 it represents an increase of 60 percent. Moreover, agricultural debt charges, taxes, and wage costs were lower in 1936. Allowance made for this additional factor would give an agricultural purchasing power still closer to that of 1929.

Certain aspects of the distribution of the farm income should be noticed. Cash income from meat animals in 1935 exceeded the corresponding figure for 1932 by 73 percent, and in the first 7 months of 1936 it advanced 27 percent over the total for the corresponding period of 1935. From dairy products in 1935 the cash income was 30 percent more than in 1932; the income from poultry and eggs was 45 percent more. These industries made small additional gains in the first 7 months of 1936. From grains the cash income in 1935 was 61 percent more than in 1932 and from cotton 46 percent more. Fruits and vegetables recorded a 41-percent gain. Income from marketings of all crops was 36 percent greater in the first 7 months of 1936 than in the corresponding period of 1935. These percentages do not include the A. A. A. payments.

With marketings and benefit payments included, the total cash income from grains in 1935 was 133 percent larger than in 1932. From cotton it was 77 percent larger. In the first 7 months of 1936 the total cash income from marketings with A. A. A. payments included was 17 percent more than in the corresponding period of 1935 though the A. A. A. payments were considerably smaller.

Regional Percentages Vary

Regional percentages of gain in 1935 over 1932 range from 33 percent in the North Atlantic States to 81 percent in the South Atlantic States. Mainly the regional differences reflect the different price behavior of various commodities, but the aftermath of the 1934 drought was a factor also. Proportionately less gain for the dairy regions than for other regions was a natural consequence of the

fact that the dairy regions had suffered less in the early years of the depression; but for the opposite reason the grain-growing areas show a relatively large increase, though reduced marketings have tended to offset the price gains.

Each of the principal agricultural regions, except the South Central States, showed an increase in income in the first 7 months of 1936, as compared with the corresponding period in 1935. In the South Central States, where smaller Government payments offset an increased return from marketings, the income was approximately the same. The gains in the other regions ranged from 14 percent in the North Atlantic, South Atlantic, and Western States to 23 percent in the West North Central States.

Accurately to measure the respective influences of the factors responsible for the recovery in farm incomes is difficult if not impossible. Mainly the improvement reflects price gains, supported by increased consumer buying power. Factors in the price gain include the revaluation of the dollar, the A. A. A. adjustment programs, the reduced production caused by the 1934 drought, and the liquidation of surpluses. In 1936 increased marketings were a factor in the income gain. Farm prices in the first 7 months of the year averaged slightly lower than in the corresponding months of 1935. In the later months, however, farm prices advanced as a result of the drought, and for the full year the farm-price average will probably exceed that of 1935.

In estimating the prospects for the longer future the most basic factor is the level of consumer incomes. Broadly, the income of agriculture varies more closely with the national income than with the level of farm prices. It is encouraging to note that the money income of the nonfarm population in August 1936 averaged 13 percent more than in August 1935 and 32 percent more than in the corresponding period of 1933. With their improved income, consumers were able to buy 7 percent more food and 12 percent more of the other items in their budget than in the previous year, but 6 and 11 percent, respectively, less of these items than in 1929. Earnings per employed worker have more than kept pace with food prices. Needless to say, farmers as a result of their income gains can deal more effectively with the consequences of the 1936 drought than they could with those of the drought of 1934.

Farm Prices and the Consumer

Effects of the drought on the cost of living will probably be similar to those produced by the drought of 1934. From crop data available in September it was estimated that for the 1936–37 season food supplies in general will be about 3 percent below the 1935–36 level, about 1 percent below the level of 1934–35, and about 5 percent below the 1925–29 average. Certain vegetables, particularly potatoes, will be in short supply. The output of fruits and vegetables and of dairy products will be lower, and after the turn of the year the supply of meats will be reduced. This will result in higher meat prices to some extent offset by seasonal declines in other food prices. In the comparable situation after the 1934 drought, retail food prices as a whole in the first half of 1935 averaged about 11 percent higher than they

did during the first half of 1934. Food constitutes only about one-third of total living costs, hence an increase of, say, 10 percent in the cost of food tends to produce a rise in total living costs of only about 3 percent.

Analysis of the trend in nonfarm income indicates that consumers' incomes in the first half of 1937 will increase at least as much as the cost of living. In other words, the purchasing power of consumers generally, in terms of goods and services, will not decline. Had there been no drought, it would have increased; and the foregoing remarks do not signify that consumers can regard with indifference the great change produced by the drought in the supply situation. But the main effect will be temporarily to arrest a gain rather than to cause a drop in the real income of consumers. Wage earners actually employed could buy with their wages more of the necessities of life in the summer of 1936 than they could in 1929 because retail prices were lower on the average. In terms of foods the purchasing power of employed workers actually advanced after 1929, when farm prices began falling. It remained above the 1929 level and reached a new high point in 1936.

In total purchasing power the position of city workers deteriorated during the first years of the depression. Pay rolls declined, while many nonfood items in the family budget remained unchanged. In 1934, 1935, and 1936, however, nonfarm labor incomes increased. These incomes for the first half of 1936 aggregated $23,492,000,000, as compared with $19,617,000,000 in the first half of 1933. More men were engaged in manufacturing in the summer of 1936 than at any previous time in the last 5 years; in July industrial production was 108 percent of the 1923–25 average, the highest point reached since November 1929. According to the seasonally adjusted index of the Federal Reserve Board, the July industrial production was 83 percent above the low point to which it fell in March 1933. The relatively small rise in the cost of living which will be the inevitable consequence of the drought will be substantially offset by recovery in urban buying power.

OUR NATIONAL AGRICULTURAL POLICY

It is commonly believed that the United States never had a truly national agricultural policy until after the World War; but the country has always had a national agricultural policy. In the period of westward migration, of rapid land settlement, and of ruthless exploitation of natural resources, the policy was negative. It was mainly one of noninterference with the private appropriation of land for use or misuse. Despite its laissez-faire character, we cannot call that procedure a mere lack of policy. It expressed a definite philosophy and, indeed, a definite program. It was what the dominant forces in the country wanted and what the majority of the people at least tacitly accepted. Our national agricultural policy in the nineteenth century reflected the belief that national welfare could best be promoted through individualism and unrestricted competition.

For a long time this theory apparently stood the test of practice. With abundant land, an open frontier, and a relatively sparse population, the quickest way to increase production, and therefore wealth,

was to get the resources into private hands. Occasionally production overshot the market; but the resulting depression did not last long and did not shake the country's faith in the exploitation program. Various administrations encouraged farming, ranching, lumbering, and other land uses through homestead laws, grazing privileges, land grants, favors to transportation companies, lenient taxation, and irrigation. Few looked forward to the closing of the frontier and to the ruthless competition that would ensue. Most people seemed to think the policy that had been adopted could be continued indefinitely.

As a matter of fact, as most people now perceive, the exploitation policy created problems that today necessitate a conservation policy. Recklessness in one age inevitably imposes prudence on the next. There are sharp contrasts between the agricultural views and programs that dominated the nineteenth century and those that shape our agricultural policy today. But the contrast does not mean that the present has broken with the past or that tradition has been sharply wrenched from its natural path. On the contrary, it signifies that cause and effect have operated normally. The new agricultural policy is the direct result of the old one and of the conditions and problems which the old policy created. As the occupation of the continent proceeded, the expansion program ran out of material. It ran out of land and forced the land hungry into submarginal farming, destructive grazing practices, and forest devastation. Land charges accumulated on the older-settled land and drove producers into overproduction. Exploitation, in short, created the need for conservation, and simultaneously excessive competition generated a need for corrective regulation. It is because our forbears went too far in one direction that we must now move in another.

No Break With Evolutionary Trend

In the transition from the old to the new agricultural philosophy there is no sudden break with the evolutionary trend, and no capricious improvisation of new doctrine. On the contrary, the link between the old exploitation and the new conservation, and between the old unregulated competition and the new principle of cooperative adjustment, is direct and close. Perhaps the authors of the exploitation program, were they here today, would disown their offspring; but the parentage can be demonstrated. After the spendthrift has wasted his money he must begin to save; after a country has squandered its natural resources it must learn to husband what remains. Our national agricultural policy since the World War has been criticized as confused and uncoordinated, but study of it will reveal a logical and indeed predestined course.

Thus the Federal Farm Board came into existence to handle surpluses left by wartime and post-war expansion. The McNary-Haugen plan, though twice vetoed, stamped its mark on subsequent legislation as a first approach to the problem of the export surplus. The A. A. A. programs were an emergency effort to substitute concerted for haphazard crop adjustments in a catastrophically falling market and to bring agriculture abreast of urban industry in the regulation of production. The new Soil Conservation and Domestic Allotment Act, though weaker in crop-adjustment power than the measure it replaced,

had the great merit of launching a positive attack on the dual problem of soil destruction and unbalanced cropping. In varying degrees all these approaches to the agricultural problem betokened a national recognition of the fact that modern problems cannot be solved by ancient formulas, and that agricultural policy today is necessarily in large measure the opposite of what it was in the period of the open frontier.

Agricultural policy draws its inspiration, not from the accidents of politics but from fundamental economic changes. In the shaping of American agricultural policy we can distinguish two great controlling forces, each of recent origin. First, of course, is the disappearance of the open frontier and the resulting pressure of population on the resources available with its threat of soil wastage and soil destruction. Second is the world-wide growth of economic regulation, not only in trade but in production. Governments are assuming greater and greater responsibilities for the regulation of commerce both domestic and foreign, and industry is becoming cartelized throughout the world. Into an economic system of that kind, a purely competitive, wholly unregulated agriculture will no longer fit. These two great forces seem destined to exert an increasing influence which will express itself in legislation and policy no matter what political party may be in power. Modern agricultural policy in the United States is not the arbitrary invention of an economic group with a special interest to promote but is a national response to an altered economic world. It is not merely an attempt to deal with temporary evils but a profound readjustment to permanently changed conditions.

Landmarks in Agricultural Policy

It is interesting to recall the contribution of the past to present agricultural policy. In 1862 Congress passed the Morrell Act, providing Federal grants of land to the States for the establishment of colleges in agriculture and the mechanic arts. After half a century of progress in agricultural technology, agriculture began to demand economic guidance. Accordingly, this Department developed extensive and varied economic services in which research was combined with the regular gathering of crop and market data, and with numerous related services such as commodity grading and standardization, and shipping- and receiving-point inspection. In 1921 these and other activities were concentrated in the Bureau of Agricultural Economics. In 1922 Congress passed the Capper-Volstead Act, giving legal recognition to the right of farmers to organize cooperative associations for the marketing of their products. In 1927 and again in 1928 Congress passed the McNary-Haugen legislation, though each time the legislation encountered a Presidential veto. Then came the Agricultural Marketing Act of 1929 and the creation of the Federal Farm Board. In 1933 the Agricultural Adjustment Act, with its provisions for processing taxes and cooperative crop adjustments, went into effect and remained in effect until the United States Supreme Court invalidated it in January last, through decisions in the Hoosac Mills and rice millers' cases. Throughout the entire period covered by this brief review American farmers manifested an in-

creasing tendency to effect organization and also to look to the Federal Government for aid in solving their economic problems.

Because of the adjustments made under the Agricultural Adjustment Act during the last 3 years and because the drought helped to liquidate certain of the surpluses, the present program under the Soil Conservation and Domestic Allotment Act is well fitted to present needs. Farmers recognize that, while this agricultural conservation program will be of immediate help in stabilizing supplies through the encouragement of more extensive uses of land, the program itself is not a direct production-control measure. A return to normal weather conditions would revive the problem of agricultural surpluses. I am inclined to believe that farmers understand what confronts them in the future and that they will look forward to making use of the method of meeting the problem of surpluses which the Supreme Court left open to them. The Soil Conservation and Domestic Allotment Act contains a provision which will facilitate this step in 1938 should farmers decide to meet their supply problem through cooperation of the States. This provision is, of course, the direct descendant of the invalidated Agricultural Adjustment Act, and preserves some of the ideas contained in that measure, as well as some of the principles developed in the application of the A. A. A. programs. It would be well, therefore, before examining methods and results under the new law, to glance back at the legacy bequeathed by the A. A. A.

Agricultural Adjustment Act Effective

It is evident, from the improvement that took place in the position of agriculture between 1932 and 1935, that the Agricultural Adjustment Act forwarded its main purpose. This was to eliminate the crushing surpluses that had piled up previously and to raise farm incomes immediately through various measures calculated to support prices. From 1932 to 1935, the period during which A. A. A. programs were in effect for cotton, wheat, tobacco, corn, and hogs, the combined farm cash income from these commodities increased 90 percent. Cash income from these five major commodities increased from $1,365,000,000 in 1932 to $2,593,000,000 in 1935. From all other farm products the cash income increased from $3,012,000,000 in 1932 to $4,307,000,000 in 1935. In 1932 the largest farm population in the Nation's history had the smallest farm cash income reported in the 26 years for which records are available. The turning point came with the adoption of the Agricultural Adjustment Act, though this measure was only one of the factors responsible for the agricultural improvement. Dollar revaluation, business recovery, credit relief extended through the Federal Farm Credit Administration, and other influences contributed. All these influences combined gave farmers in 1935 a cash income available for living larger than in any year since 1929. They had to pay somewhat more for goods and services in 1935 than they did in 1932, but with allowance made for that, the purchasing power of the farm cash income in 1935 was still 35 percent larger than it had been in 1932.

The great drought of 1934, which cut our production of feedstuffs in half, necessitated modifications in the A. A. A. program so as to

encourage production of emergency feed crops that year and to provide for certain increases in production the next. It became advisable also to work toward a better coordination of the various commodity programs and to provide for greater regional and area differences so as to promote good farm management and good land use. Certain shortcomings had developed in the emergency application of the programs, notably a tendency to fix or freeze production in the historic mold, without proper regard for the changing requirements of different areas. But the crop-adjustment programs had shown themselves to be useful in promoting soil conservation and good farming. They fostered some shift from soil-depleting cash crops, such as cotton and wheat and corn, to soil-building crops such as grasses and legumes.

To strengthen and develop this favorable tendency, the A. A. A., working with the State experiment stations and with other branches of this Department, launched studies in regional planning and modified its crop-adjustment contracts with farmers. It began to place less emphasis on flat percentage changes in production and more on differential adjustments to the requirements of local as well as of national conditions. In this way the A. A. A. developed principles which found continued application when the invalidation of processing tax and production control provisions of the Agricultural Adjustment Act led Congress to pass the Soil Conservation and Domestic Allotment Act. Under the A. A. A. the primary objective was production control, with soil conservation a secondary though increasingly important object. Under the new law soil conservation becomes the primary aim, with some crop adjustments coming as a byproduct. Probably in a period of good crops and high yields the degree of crop control attainable under the new measure will not be adequate, but for the time being it works for a better crop balance. The emphasis it puts on grass and legumes has the double advantage of making our agricultural system less intensive, while at the same time conserving soil wealth.

Methods Under New Law

Under the Soil Conservation and Domestic Allotment Act the Federal Government in 1936 made grants to farmers cooperating in soil-conserving and soil-building programs. It did not make use of contracts. Cooperating farmers simply planned their operations in line with definite soil-conservation standards, worked out with producers, soil specialists, and State agricultural leaders. They obtained their grants after officials had checked the performance with the standards. For this purpose Congress made $470,000,000 available for the year, the goal for which was to have 130,000,000 acres in soil-conserving crops as compared with 100,000,000 acres in 1930. Though the program for the year was national in scope, the country was divided for administrative purposes into five regions—the northeastern, the east central, the southern, the western, and the north central—and the practices for which payments were made and conditions which had to be met were varied so as to meet the particular needs of the farmers in each region.

After January 1, 1938, the program will enter upon a State-aid phase; in other words, the Federal Government thereafter will make soil-conservation grants, not directly to individual farmers, but to the States for distribution to cooperating farmers. The Soil Conservation and Domestic Allotment Act sets up five objectives: Preservation of soil fertility, diminution of soil exploitation, promotion of the economic use of land, the protection of rivers and harbors against the results of soil erosion, and the attainment of parity income for agriculture. Power to promote the last-named object will not be available until the State-aid phase of the act goes into effect, but economists and farm-management specialists are already studying the means by which it may be used, provided it is needed.

Soil conservation and good farm management were important objectives under the A. A. A. programs. As experience showed the need, the A. A. A. modified its original requirements so as to give contracting farmers more scope in combining their various crop enterprises in harmony with the national crop-adjustment programs and more incentive to protect and restore soil values. In the north-central region, for example, from two-thirds to three-fourths of the acreage diverted from corn, wheat, cotton, and tobacco went into legumes and grasses. This diversion, though of a temporary nature, was a good beginning in cooperative soil conservation. It was the first large-scale effort to correct the bad effects of cropping practices developed in the wartime and post-war booms, when much land not suited to continuous intensive cultivation was brought under the plow. In the South, farmers were allowed to increase their acreage and production of food and feed crops, which meant an increase in the farm standard of living.

The necessity for soil-conserving practices was long overdue. Soil depletion had characterized American agriculture for decades, and the overcropping which took place during and after the World War made matters worse. Though the demand for farm products declined in the twenties, and though farmers had apparently a strong motive to alter their cropping systems, the acreage of cultivated, soil-depleting crops continued to increase. Burdened with debt and driven by low prices to seek compensation through more and more production, farmers kept on mining the soil. The A. A. A. enabled them to adopt a better course. With higher prices and benefit payments in view, they could begin to think of their permanent, as well as of their immediate, interest in the land and, to some extent, could stop selling the fertility of the soil piecemeal with the crops at low prices to foreign countries.

Research and Demonstration Authorized

The soil problem received special recognition when Congress passed the Soil Conservation Act of 1935, which provided for a general program of research and demonstration to be conducted by the Soil Conservation Service in cooperation with the State experiment stations and with farmers. Broadened and amended after the Hoosac Mills decision, the measure evolved into the Soil Conservation and Domestic Allotment Act. This act recognizes a social as well as an individual interest in soil conservation and provides the individual

farmer with means to advance both interests simultaneously. It facilitates a concerted effort to correct the grave mistakes that have been made in the past, and particularly since the World War, in the use of farm land.

Much of the land that came under the plow for the first time during and after the World War lies in the western Great Plains, and cannot be expected in normal circumstances to give profitable yields. Moreover, it is extremely subject to wind erosion. In the older cultivated regions, especially in the Corn Belt and South, there is heavy overcropping. In the Corn Belt, according to a report of the National Resources Board, overcropping is a major soils problem, particularly on the erosible land along the eastern edge of the sand hills, the plains of southern Nebraska, and the hilly areas of southern Iowa, northern Missouri, and western Illinois. Overcropping in this area is damaging more than 36,000,000 acres of farm land. Besides exposing the land to erosion, it is making soil harder to work, reducing the plant-food content and exposing land to increased danger of drought. Erosion and the drastic depletion of soil fertility due to overcropping are common throughout the South, and erosion is far from unknown in New England, even though much of the farm land is already in soil-conserving crops.

What is happening to farm lands throughout wide areas may be indicated by the results of experiments on the historic Morrow plots at the University of Illinois. One comparatively level plot which had been continuously in corn and oats for 23 years lost 4 tons of humus per acre, and yields steadily declined. On another plot, on which corn, oats, and clover were rotated, and on which fertilizers were applied, the soil retained 14 tons more of organic matter per acre than did the soil of the corn-and-oats plot. Studies in Ohio revealed that during the last 60 years the adoption of better varieties, better seed, and scientific methods for the control of insects and plant pests merely balanced the downward trend in the average productivity of the soil. In other words, more than half a century of applied science showed no net gain because it did not include effective soil conservation. Comparable studies in Iowa demonstrated that present farm practices will not maintain the fertility of the soil and control erosion, and that in order to do so it will be necessary to reduce the corn acreage considerably. On rolling land the major problem is soil washing. Land cropped continuously in corn, in soil tests at the University of Missouri, lost seven times as much soil as land planted to a rotation of corn, wheat, and clover, though the slope was only 4 percent. Land kept in bluegrass lost only one-sixtieth as much soil as that kept in continuous corn.

Soil Depletion in the South

Because of the system of farming followed in the South, the soil has been greatly depleted. Southern farmers devote a larger percentage of their cropland to soil-depleting crops than do farmers in any other part of the country. In the nine States of the southern region, with the exception of Florida, the ratio of soil-depleting cropland to the total cropland ranges from 76 to 92 percent and averages approximately 80 percent. The large percentage of clean-

tilled row crops is a heavy drain on soil resources. In acreage cotton and corn are the principal crops, though there is a considerable acreage of wheat in Oklahoma and Texas. Cotton and corn both leave the land comparatively bare in the winter and subject to soil erosion. The mild climate and the heavy rainfall aggravate the problem.

In 1936 the nine States shifted about 13 million acres from soil-depleting commercial crops to soil-conserving noncommercial crops. This was more than 40 percent of the total acreage so diverted in the United States. Soil conservation in the South calls for a relatively large percentage of diversion. But the dense farm population and, in recent years, the low price of cotton have made the operation difficult. Eleven million people, or one-third of our farm population, live in the nine States included in the southern region.

Prior to 1936 this situation was alleviated to some extent by the agricultural adjustment programs, which embodied a number of soil-conserving features; and in 1934 and 1935 about 14 million acres normally in cotton was shifted to the production of food and feed crops, and to crops that conserve the soil. The acreage of soil-conserving crops in the South in 1936 was the largest on record.

In setting up the soil-conservation program in the western region it was necessary to take into consideration a great diversity of crops, of types of farming, and of farming practices. This region comprises Arizona, California, Colorado, Idaho, Kansas, Montana, New Mexico, Nevada, North Dakota, Oregon, Utah, Washington, and Wyoming. In the more humid areas the major problem is that of preventing erosion by water, while in the Great Plains erosion by wind demands attention. The so-called dry-land area requires special safeguards. Irrigation farming has its peculiar problems. In parts of Oregon, Washington, and northern Idaho summer fallowing enters into the system of farming and calls for appropriate conservation practices. In certain areas payments were made for contour cultivation, and particularly for contour listing, which tends to check erosion by both wind and water. Where wind erosion is serious, strip cropping and strip fallowing were encouraged. In three States payments were made for the use of lime or gypsum in soil building; and in States where noxious weeds are very prevalent, weed-control measures were regarded as a soil-building practice.

Organization for the Program

The organization set-up for carrying out this year's program retained the principle of farmer cooperation, which had been developed under the A. A. A. programs in 1934 and 1935. As a coordinating body between the Federal Administration and local bodies there was established for each State a State agricultural conservation committee. This consisted of from three to five members, appointed from more or less distinct type-of-farming areas. The State committees generally exercised advisory and supervisory functions. They assumed the responsibility for checking the work of the county committees in establishing bases for supervising the checking of performance by cooperating farmers and for reviewing county expenditures

and program disbursements. They were also responsible for the relative cost, operation, and the effectiveness of the programs.

Within the counties the organization was similar to that established under the earlier A. A. A. programs. Each county had its county and community committeemen, all of them farmers. These committeemen were elected by their neighbors in each township or other similarly defined area, to assist program participants in executing work sheets and in planning their farming operations in line with conservation standards. Also, the township committeemen helped, at the end of the season, to check performance and to certify the claims of cooperating farmers for Federal grants. Responsibility for supervising and coordinating the work of the various community committeemen, for reviewing program forms and documents, and for making final recommendations for the adjustment of individual "soil-depleting bases" within the prescribed limits for the county, rested with the county committee, which accordingly had authority to investigate local problems. Educational work necessary in the explanation and application of the programs was under the direction of the State agricultural extension services, which also were given large administrative duties in the West and South.

In determining an individual farmer's contribution to the national soil-conservation goal and therefore establishing the amount of his claim upon the grant funds available the starting point was the soil-depleting base. Cropland uses were divided into two major classifications, soil-depleting and soil-conserving. Among the soil-depleting crops may be mentioned corn; small grains harvested for grain or hay, or seeded alone and pastured; annual grasses pastured or harvested for grain or hay; soybeans, cowpeas, and field beans if harvested for grain; the sorghums, potatoes, commercial truck and vegetable crops, sugar beets, tobacco, and cotton. In the soil-conserving category were included most of the legumes and perennial grasses; soybeans, field beans, cowpeas or field peas, if these crops were turned under as green manure; small-grain crops if turned under as green manure and followed by soil-conserving crops; orchards and vineyards interplanted with winter cover crops; acreages summer-fallowed if followed with soil-conserving crops. The two categories include many crops not here mentioned. Those cited merely illustrate the principle. After drought conditions developed in June and July, the Administration authorized many changes and additions to the crop classifications so as to meet the unexpected weather conditions.

For the farm owner or operator who planned to cooperate, the county committees established a general soil-depleting base, and in the South special bases were established for cotton, tobacco, and peanuts. This base represented a normal acreage of the soil-depleting crops on the farm, with the total acreage serving as the starting point. The county limit was the ratio of the soil-depleting crop acreage to all farm land or to all cropland in the county. As representing the most normal period for the production of soil-depleting crops in recent years, the north-central region took 1932 and 1933 as the base years for establishing the county limits, the western and southern regions took 1928–32, and other regions adopted different base years. County

committees notified farmers of their preliminary bases, but these were not necessarily final. Farmers had the right to appeal for reconsideration of their bases, first to the county committee and then to the State committee. This appeal procedure, besides being consistent with the democratic principle underlying the whole program, permitted the correction of unintentional errors. By taking all possible precautions to have the bases fairly established, the Administration hoped that they would prove satisfactory not only for the current year but for subsequent programs.

Two Classes of Payments

Farmers cooperating in the soil-conservation program could qualify in 1936 for either or both of two classes of payments, the class 1 or soil-conserving payment, and the class 2 or soil-building payments. The class 1 payment was available to farmers who diverted a portion of their soil-depleting base acreage to soil-conserving crops or uses. Farmers were eligible to receive this payment on any number of acres up to 15 percent of their general soil-depleting bases, up to 35 percent of their cotton bases, 30 percent of their tobacco bases, and 20 percent of their peanut bases. It was determined on a per-acre basis and averaged approximately $10 an acre for the entire country, varying quite widely, of course, with variations in the productivity of different counties and of different farms. Farmers desiring to qualify for the class 2 or soil-building payment had to adopt certain approved practices calculated to restore soil fertility.

These practices varied in different parts of the country but generally included new seedings of legumes and perennial grasses, seeding of soybeans, cowpeas, etc., for green manure, and applications of limestone. In certain dry areas farmers could qualify for small per-acre payments if they planted rye as a nurse crop for pasture grasses or if they strip-fallowed in such a way as to check wind erosion. In some areas payments were made for terracing. There was a top limit on the total amount of class 2 payments that a cooperating farmer might receive, which was generally the same number of dollars as there were acres of soil-conserving crops on cropland on his farm in 1936. Hence the larger the acreage of soil-conserving crops on the farm in 1936 the larger the soil-building allowance. A farmer could earn all or part of the allowance, in proportion to the extent to which he applied the recommended practices.

The farmer's response to the agricultural-conservation program has been gratifying. Although the entire program had to be developed after the signing of the Soil Conservation and Domestic Allotment Act on February 29, more farmers applied for work sheets or asked for bases to be established than cooperated in the several commodity programs under the A. A. A. In general the cooperation was about the same as under the A. A. A. in those areas where corn, cotton, wheat, and tobacco were the major crops, and much greater in those areas where general and mixed farming is found, as, for example, in dairy regions like Wisconsin and New England and the mixed-farming sections in California. This, of course, was due to the fact that the new program was much more flexible than the old com-

modity programs, that it was better regionalized, and that each farm was considered as a unit.

As already indicated, the primary aim of the new program is the conservation and improvement of the soil, with crop control an incidental byproduct. With the move next year from a Federal to a State-aid basis, crop adjustment may become more important. When the States disburse the soil-conservation grants, soil conservation and crop adjustment may be combined legally. In fact, the two principles go naturally together. There was a steady growth of soil conservation under the original A. A. A. programs, and there should be a similarly steady growth of crop control when the national program for soil conservation gets well advanced. For it is obvious that the shift from soil-depleting to soil-conserving crops answers not only the needs of the soil but also the needs of the permanent agricultural market.

The shift from soil-depleting crops, such as cotton, tobacco, and wheat, to soil-conserving crops, including primarily hay and forage, may go along with an increase in the animal enterprises commonly using the latter crops, particularly the beef and dairy enterprises. This tendency the present drought partially obscures. An increase in the relative output of these two enterprises, particularly dairying, appears desirable from the national point of view. But it should be recognized that farmers in the major dairy areas have long followed farm practices and cropping systems of a soil-conserving and soil-building character. Care must be taken not to work a disadvantage upon them. This problem has been attacked by continued efforts to secure orderly and stabilized fluid-milk markets through marketing agreements and orders, through the purchase of price-depressing temporary surpluses and their distribution through relief channels, and through the elimination of cattle infected with Bang's disease and tuberculosis. In addition payment for practices of a soil-improving character enables these farmers to improve their pastures and hay lands.

Long-Time Effects on Production

The present phase of drought-caused shortage can only be temporary. Under normal weather conditions our agricultural industry can oversupply its market, and the natural reaction from the present drought will be for it to do so. For the moment it may seem premature to talk again about overproduction, but experience proves that under blind competition one or two good crop years can pile up surpluses.

It will be well to remember, when overproduction impends, that soil conservation alone is not a sufficient preventive. Soil-conservation practices tend to have more effect on output at first than they do later. In their early stages they reduce the average intensity of cultivation significantly, and therefore the tendency to oversupply the market. Eventually, however, they increase soil productivity; it is obvious, moreover, that less intensive cultivation of part of the farm area may promote more intensive cultivation of the remainder, particularly if the farm population is excessive. Unless the foreign as well as the domestic demand for American agricultural products revives, the rehabilitation of the soil through soil-conservation programs will combine with other factors in the agricultural situation

to confront the country again in the near future with the absolute necessity of establishing a good adjustment between production and market requirements. Permanent agricultural policy should achieve soil conservation, consumer protection, and crop control together.

The transition from emergency crop adjustments to a more permanent program, with good land use and higher current incomes ranking equally as objectives, began in 1935, nearly a year before the Supreme Court decided the Hoosac Mills case. It started with a regional-research project undertaken by this Department in cooperation with the land-grant colleges and the State experiment stations.

Farm-management specialists had recognized that a shift toward less-intensive cropping, accompanied by soil conservation and soil building would reduce surpluses and at the same time lower the costs of production. They did not know, however, exactly what adjustments were necessary in cropping systems. Neither did they know what the effect of specific regional changes would be on total production. The research project sought light on these questions.

At the same time that it sought the advice of the experiment stations, the Department asked farmers for their recommendations. It did so through a county-planning project, which was in full swing by the fall of 1936. Committees of farmers were formed in 2,500 agricultural counties throughout the United States. These committees offered opinions on the same questions that were asked of the experiment-station specialists. They estimated the county adjustments apparently necessary in crop and livestock systems to maintain soil fertility, control erosion, and promote more efficient farm management.

Specialists in the Department and in the State experiment stations are summarizing the results. The estimates of the farmers are being combined by type-of-farming areas, so that they may be compared directly with the estimates of the experiment station specialists. It will then be possible to arrive at final estimates which will command the agreement of both the farmers and the experiment station group. This year the farmers' committees studied the apparent results of the soil-conservation program, and offered suggestions for its improvement.

This work with the farmers and the technical specialists reflects the Department's recognition of the importance of drawing on the knowledge and experience of local groups in formulating national agricultural programs. Reliance on local interest and cooperation is more necessary now than ever, because the shift from crop control to soil conservation enhances the importance of local knowledge and local action. There was considerable decentralization of administrative responsibility under the original A. A. A. programs. There must be considerably more in planning agriculture on the new basis. In no other way can the procedure be at once efficient and democratic.

METHODS OF EROSION CONTROL

This year's exceptional weather drew attention forcibly to the need for a regional and local, as well as a national, approach to the problem of the soil. Floods in the Northeast and elsewhere and dust

storms in the Great Plains demonstrated that in some areas all the land should be brought under uniform programs for the control of erosion. Operations launched under the Soil Conservation and Domestic Allotment Act moved in the desired direction, but the national approach cannot do everything that is necessary.

There is need also for intensive local operations in which each farm may be treated as part of a regional pattern. As is well known, good soil care on one farm may be counteracted by neglectful methods on neighboring farms. Efficient soil conservation cannot be promoted merely by the action of individual farmers; it requires coordinated effort through entire land-use regions.

Research, demonstration, and operations in this field are the special tasks of the Soil Conservation Service, which was established in 1933 in the Department of the Interior and transferred 2 years later to the Department of Agriculture. This Bureau cooperates in research with other Federal agencies as well as with the State agricultural experiment stations. It cooperates also with the Extension Service in the development of demonstration projects and in educational matters relating to erosion control. Essentially the methods of the Soil Conservation Service are intensive. It makes detailed surveys and studies the erosion conditions of entire land-use regions as a basis for specific recommendations and preventive practices.

The studies include topographical and contour mapping, erosion surveys, soil analyses, observations of land-use practices, and the testing of different expedients and practices. The demonstration projects accomplish three distinct purposes: They test various methods of erosion control, provide demonstrations of the appropriate methods, and actually prevent erosion on the particular lands involved. All available methods, such as correct cropping and rotations, tillage and engineering practices, moisture conservation, and pasture and forest development are applied in combination.

Mistaken land-use practices in the United States have caused the ruin by erosion of some 50,000,000 acres and seriously damaged 50,000,000 acres more. Much additional land is in danger. Soil erosion injures not merely the owners or the occupants of the eroded lands and their immediate neighbors; its harmful consequences extend through whole watersheds and throughout the country. Erosion dissipates fertile soil in dust storms, piles up soil on lower slopes, covers rich bottom land with poor subsoil, destroys food and cover for wildlife, and increases flood hazards. Furthermore, it causes the silting and sedimentation of stream channels, reservoirs, dams, ditches, and harbors, and damages roads, railways, irrigation works, power plants, and public water supplies. It is a public as well as a private liability, and it can be dealt with effectively only by cooperative endeavor.

Soil Losses Heavy in 1936

Soil losses from the floods last spring were tremendous in the Northeast and in Texas and Colorado. Soil blowing in the Great Plains, with reduction of the vegetative cover, emphasized the need for a radical change in the farm system in certain areas, as well as for compre-

hensive soil-conserving programs. These conditions brought home to farmers generally, and to other interested groups, the fact that the soil problem has distinct regional and local peculiarities, the treatment of which requires methods appropriate to each region and each locality. Visible damage left by the floods and dust storms was only a fraction of the total damage, but it emphasized the helplessness of individual farmers in dealing with conditions that affect entire land-use regions.

Even in New England, much of which is forest-clad or in pasture, there is preventable erosion. Perhaps the most serious and widespread damage in 1936 occurred in the cotton States from North Carolina to Oklahoma and Texas. Overcropping caused erosion in the Corn Belt and overgrazing and overplowing were main soil hazards in the Great Plains. In certain regions the cultivation of steep slopes and the practice of setting brush fires did great harm. In some localities the most urgent need is for engineering work such as terraces, check dams, ditches, and ponds, and in all localities there is need for adjustment in tillage practices. In some areas the problem is principally one of clothing denuded slopes with vegetation or of increasing the ratio of soil-conserving to soil-depleting crops. Everywhere, however, the problem has local peculiarities which interdict the use of blanket methods.

In the demonstration projects, 139 of which have been established in 41 States, the Soil Conservation Service begins by marking off a naturally bounded tract about 25,000 acres in extent. (There are three very large public-land projects in the Southwest and one in Wyoming, but these are not typical.) Next follow various soil and farm-management studies, including analyses of cropping systems and farm-income conditions. The results become the basis for a soil-conservation plan applicable to the demonstration area, to which the Soil Conservation Service gives effect by two principal means.

(1) It reaches an understanding with the proper public agencies that may be involved; then (2) it enters into 5-year agreements with private landowners. Each agreement contains a plan for land use and appropriate practices, specifies the assistance to be given by the Service and the proportion of the work to be done by the farmer, and obligates the operator or owner to maintain for the 5-year period any improvements that may be constructed and also to follow the agreed program of cropping and tillage. The Soil Conservation Service also draws up land-use programs for the entire area, including land not in farms as well as the land in actual cultivation.

Yet work of this type touches directly only the fringe of the problem. It covers only a fraction of the Nation's farm land, and directly involves a comparatively small number of farmers. Compared with what needs to be done, the amount of erosion control effected is very small. Research results and practical recommendations reach a wide audience through the extension services and find application on millions of farms in the national soil-conservation programs. Nevertheless much remains to be done. There is need for cooperation not only between the Federal and State agencies but between these agencies and local farm groups.

Soil Conservation Associations

Accordingly, besides conducting demonstration projects and carrying on similar work with Emergency Conservation Work camps, the Soil Conservation Service is encouraging soil-conservation associations, more than 400 of which have been organized already. Most of them are on or near areas where there are demonstration projects or where Emergency Conservation Work projects are under way. Membership in an association ranges from 10 to 400 farmers. It is entirely voluntary, and most of the associations have adopted articles of association without formal organization. They have the legal status of partnerships for limited purposes. Their members agree to live up to certain cropping and tillage practices and to cooperate in operations requiring concerted effort, such as the construction of terraces, check dams, ponds, and ditches.

There is a fundamental relationship between soil erosion and land-use practices on both farm and nonfarm land. It does not suffice to check erosion on farms here and there if other farms nearby continue to erode. Improper slope cultivation, with consequent heavy erosion, may ruin a whole valley lower down. In other words, the problem of preventing soil erosion is a social as well as an individual problem, and the soil-conservation associations rest on this principle. The organized farmers of an entire land-use area make a united attack on a problem which they could not solve individually.

In tackling the problem of the soil, however, voluntary organizations of the kind above described have obvious limitations. At the request of State agencies this Department has prepared a standard State conservation-districts law to serve as a recommendation regarding the nature of appropriate legislation, which, if enacted by State legislatures, would authorize the formation of public agencies with power to enter into agreement with farmers relating to the performance of appropriate control operations on eroding lands, and in case of majority vote, to establish land-use regulations. Texas has passed such legislation, providing authority to wind-erosion districts to expend funds and carry on work on lands not properly treated by the owners. In that State 14 conservation districts have been organized. Several other States are considering the enactment of similar laws at the next sessions of their legislatures.

The standard measure provides that proposed land-use regulations must be submitted to a referendum of the land occupiers and may not be enacted without a favorable majority vote. Once approved, the regulations would be binding on all lands within the district. There are provisions for notice, hearing, referenda, administrative appeal, and judicial review. No district could be organized without a majority in favor of it, and no specific regulation could be imposed without a referendum.

Boundaries of the conservation districts would be determined by a State soil-conservation committee, which could not act, however, until a petition had been filed with it by at least 25 farmers and until a public hearing had been held. The committee would fix the district boundaries by a State plan, drawn up to indicate the soil, the topography, and the types of farming. Once organized, the dis-

trict would have the authority to accept funds and services and otherwise to cooperate with Governmental agencies in the development of plans and programs for the district.

It would receive an annual appropriation from the State legislature, and technical and other assistance from both State and Federal agencies. It would have the power to make intensive studies of its territory and to contract with farmers for the performance of necessary control work. Wide adoption of this plan would provide the opportunity to develop erosion-control operations on an intensive local basis as a useful and, indeed, necessary complement to the more general agricultural conservation program instituted under the Soil Conservation and Domestic Allotment Act.

Land Use and Flood Control

In the Flood Control Act, which was approved June 22, 1936, Congress recognized the importance of land-use methods in flood control. Floods, of course, are erosion phenomena. They waste soil as well as water. The new law provides that Federal investigation of watersheds, measures for run-off and water-flow regulation, and measures for the prevention of soil erosion on watersheds shall be instituted by the Department of Agriculture. Studies and projects relating to the improvement of rivers and other waterways for flood control are the responsibility of the War Department. The act declares it to be the sense of Congress that flood control on navigable waters or their tributaries is a proper activity of the Federal Government in cooperation with the States and their political subdivisions, and that investigations looking to the protection of watersheds are in the general welfare. Thus the act emphasizes the complexity of the flood problem and points to the necessity for an approach to it from an agricultural as well as from an engineering standpoint.

LAND POLICY

It is coming to be generally recognized that the cornerstone of a sound national economy is a rational land policy. The droughts of recent years, with the resulting soil blowing and dust storms, have focused attention on the need of long-time land-use planning. Needless to say, wind erosion is not the only indication of the need. Forest devastation, the progress of soil erosion by water, the wide extent of submarginal farming on land unsuited to farming, the growing seriousness of tenure problems in many areas, and the prevalence of destructive cropping and overgrazing are a few of the problems which betoken the want of a coordinated land policy. Fortunately we have made a good start in recent years toward the development of a socially desirable land-utilization program.

The Resettlement Administration has begun to acquire poor farm lands and to promote their development for other uses. It has also aided farm people in some areas to find better locations. In the last fiscal year the Resettlement Administration obtained options on 9,500,000 acres of poor farm land in 207 projects. On the bulk of this acreage the Administration took up the options at an average price of about $4.50 an acre. Approximately $38,000,000 has been already allotted for the conservational development of these lands,

and the undertaking gave employment to as many as 55,000 relief workers.

Among the 207 projects 46 were sponsored by the National Park Service of the Department of the Interior. These will be developed for recreational purposes. The Bureau of Biological Survey has sponsored 32 of the projects for the propagation and protection of migratory waterfowl. The Indian Service has sponsored 31 projects to provide more land for Indians. The Resettlement Administration has sponsored 96 projects primarily of an agricultural character, though some of them include recreation, wildlife, and forestry aspects. In its resettlement activities the Resettlement Administration has approved 97 projects calling for the purchase of 730,000 acres of land and the building of homes for 13,255 families. Funds are now available for the construction of 40 of these projects. In addition there are 43 subsistence-homestead communities either completed or in process of completion.

As noted elsewhere in this report, the Bureau of Biological Survey has acquired considerable land for the preservation and conservation of wildlife. Prior to 1933 it had purchased 215,365 acres with funds appropriated to it by Congress. These lands formed the nucleus for 11 wildlife refuges, within which, however, additional lands were needed. Since 1933 the Biological Survey has purchased considerably more land with emergency funds made available through the Resettlement Administration. On July 1 about 893,000 acres in 42 refuge units had been, or were being, acquired at a total land cost of $5,359,254. Another important aspect of the national land policy is being developed under the Taylor Grazing Act, which Congress amended last year in important respects. One amendment enlarged (from 80,000,000 to 142,000,000 acres) the area of vacant unappropriated and unreserved lands of the public domain available for the creation of grazing districts under the act, which is administered by the Department of the Interior.

Land settlement, as well as the diversion of poor farm land to other uses, forms an integral part of the national land policy. Land settlement or resettlement will doubtless continue as long as we have suitable land available. Between 1930 and 1935, according to the Census of Agriculture, the number of farms in the country increased by approximately half a million. This is an indication of the extent to which farming has cushioned the shock of the industrial depression. Industrial workers have established many of the new farms in and near industrial centers, but a larger proportion of the increase has resulted from the fact that in the depression years the natural increase of the farm population could not find nonfarm employment. The new farms have developed largely on self-sufficing lines. Part-time farming underwent considerable development. Numbers of industrial workers acquired small plots near their work. They produced some of their own food and something to sell besides, and reduced their living expenses in other ways. Many suburban families started small-scale farming without moving. Some of them were able to rent land near their homes. This whole movement caused the census to classify as farms many places which previously it had not so classified.

Return Migration to Submarginal Lands

Another major type of recent land settlement is taking place on the poorer farm lands in several regions. In these areas, the chief of which are the southern Appalachian, the Lake States cut-over, and the Ozarks, considerable migration and farm abandonment had previously taken place. After 1930, however, many of the people who had gone away returned. They had lost their city jobs, and their former farm homes offered them at least a subsistence. But in some areas the part-time nonfarm work that had previously been available could no longer be obtained. Many lumbering and mining industries had collapsed. As a result the rural folk had to depend more than ever upon farming. The number of both part-time and full-time farmers increased. Furthermore, these areas have normally a high birth rate and there was no place for the rising generation to go. In consequence the rate of increase in the number of farms was greater in these areas than over the country as a whole. As a matter of fact, there was relatively little new settlement in the better commercial farming areas. In some such areas, indeed, as for example in central Indiana and Illinois, the farm population decreased, and farms became larger.

This tendency toward an increase in the number of farms in poor farm areas inevitably created difficult problems. It is not an easy matter to start a new farm and get it well established even in good times. In hard times, particularly where the land is poor and where the settlers have little money, the obstacles are greater. Many farmers who returned to their former homes, or who took up other land, found themselves unable to make ends meet.

Small, poor farms inadequately stocked and equipped do not furnish an easy livelihood, and the occupants will be quick to move when better prospects appear. The Resettlement Administration is studying the problem and, where possible, is providing opportunities for the relocation of farm families on land better suited to their needs. The creation of new farms in regions of poor land, where soil depletion is serious and where the standard of public services is low, simply means the creation of rural slums. The new farms established in the last few years have commonly been smaller and poorer than the old ones, and sufficient additional part-time work can seldom be had. Resettlement alone cannot cure the trouble, though it may help. More is to be hoped for from the revival of industry, which will tend to lessen the pressure of population on the land; but unless employment opportunities in industry can be stabilized we shall continue to face the problems created by the periodic swings of a large segment of our rural population back and forth between country and city, moving cityward in good times and countryward in periods of depression.

The development of better land use is largely dependent on the improvement of land-tenure systems. Most people now recognize that not all the land should be in private hands. Public ownership is better for parks, for various recreational uses, for wildlife refuges, and frequently for forests. Certain types of grasslands, as well as forest lands, can be best managed as public property. These facts,

which scarcely anyone now denies, do not warrant going to extremes in the public ownership of land resources. They simply indicate that the public ownership of land has a place in a good land system, and that tradition and custom should not be allowed to block reform.

There are good and bad methods of private ownership. Certain widely established practices stimulate unwise speculation, soil mining, absentee landlordism, and excessively high rates of tenancy. These are not the inseparable and unavoidable results of private ownership. Methods can be developed which tend to minimize them, as the experience of some other countries amply demonstrates. Our traditional land-tenure system has shortcomings which can be remedied without changing its fundamental character. But it is necessary to recognize that there are different types of land, some of which can best be used as private property and some of which can best be used in public ownership.

Conditions Peculiar to United States

It is necessary also to recognize that the tenure practices developed in this country are not the only practices available. Our methods of private ownership have developed tenancy conditions very different from those of some other countries. Thousands of our farm tenants change their farms every year, and thousands more have only the semblance of security in their tenure. Few tenant farmers, except those who occupy the farms of relatives, can be sure of operating their farms for longer than the period covered by the lease, which is generally for only one crop-year. Moreover, they have no stake in any improvements which they may make on the farms. If they keep the buildings and equipment in good repair and build up the soil through good tillage or the application of fertilizer, or if they prevent erosion by terracing or other methods, they may have their rent raised. Should they be forced to leave they will not be compensated for the improvements. This fact discourages tenants from making farm improvements and from conserving the soil. The new Soil Conservation and Domestic Allotment Act is seriously handicapped in its application to tenant farmers by these difficulties.

Other countries have taken steps to reduce tenancy or to change and improve it, and eventually the United States must do the same. It must face the problem of providing security for its great mass of landless farm people. The farm census of 1935 reported about 2,865,000 tenant farmers, whose families aggregated 12,500,000 people. This was the largest number of tenant farmers ever reported by the census. In most States the percentage of tenancy increased significantly between 1930 and 1935. In certain areas more than two-thirds of the farm operators are tenants. Many of them frequently shift from farm to farm to the injury of the land, to the deterioration of community institutions, and to the decline of their own morale. Also, our farm population includes several million farm laborers, a large proportion of whom lead a migratory life, with only casual and uncertain employment. This group, as well as the tenants, should be considered in our land policy.

This Department, in cooperation with the Resettlement Administration and other agencies, is studying ways and means of improving

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the tenancy system. The problem is national in scope and of tremendous importance. In some areas an acceptable remedy would be a more widespread diffusion of farm ownership provided such ownership can be protected from the worst vicissitudes of our economic life. One of the Resettlement Administration's projects seeks to aid 1,000 southern tenants to become farm owners. Then there are ways of improving leasing agreements. It should be possible to do so with advantage to landlords as well as tenants. The problem is to reshape our land-tenure system so as to promote a type of agriculture calculated to conserve the soil, to give the cultivator a more secure occupancy of his farm, to maintain the existing capital investment in farm buildings and farm improvements, and to promote the development of sound rural institutions. Most of the necessary steps will require legislative action, both State and Federal. The whole problem requires statesmanlike treatment.

Farm-Land Values

Farm-land values increased for the third successive year during the year ended March 1, 1936. This gain, of course, reflected continued improvement in agricultural conditions. Not only were valuations higher, but the farm-land market indicated increased interest on the part of prospective farm buyers, particularly in the East North Central and Pacific States. The number of farms purchased increased considerably. With the equities of farm owners rising, loan companies showed more willingness to finance sales; sellers raised their asking prices, and creditor agencies found themselves able to dispose of more farms. Tenants showed a definite interest in buying farms.

This Department's index of the value per acre of farm real estate rose during the period mentioned from 79 to 82 percent of the pre-war level. Gains were far more general than in either of the 2 preceding years. All States but two reported some increase. During the preceding year only 31 States reported rising values. As a group the Corn Belt States reported the greatest average increase, nearly 8 percent. States in the wheat region and grazing area of the West averaged 5-percent gains. The Cotton Belt States averaged 3 percent; the hay and dairy States averaged 2 percent. For 11 States the index was above the pre-war basis. Four of these States were in New England; one in the Middle Atlantic group of States; five in the South, and one on the Pacific coast.

There were favorable changes in the frequency of transfer. For the country as a whole the number of farms transferred as a result of debt difficulties was a little smaller than during the preceding year, though the decline was not uniform. In fact, in a number of States such transfers increased. For the country as a whole, however, forced transfers associated with debt declined from an estimated frequency of 21.0 to 20.3 per thousand of all farms. The number of voluntary transfers showed a definite upturn and reached levels comparing favorably with those of the years immediately preceding the depression. This gain, though somewhat encouraging, did not indicate that a wholly normal farm real-estate market had become reestablished. Creditor agencies still had many farms which

they were anxious to sell. Nevertheless, the emergency phases of land financing declined in importance.

From the standpoint of the individual farmer attention now shifts to making good on present loans and to securing normal financing at reasonable cost. The Farm Credit Administration is giving substantial help. Its activities in refinancing, in the deferring of payments on principal, in the granting of extensions in facilitating the handling of distressed mortgage debts, and in reducing interest costs to farmers are important factors in the improvement of the farm real-estate situation, as well as in the improvement of agriculture as a whole. How effective this work has been can be seen in the decline in the number of farmers who need aid in preventing foreclosures and also in the decline in the number of extensions granted. Also, collections on loans held by the land banks are improving. The important task now is to develop a farm-mortgage system that will be more nearly shock proof than the system that existed before the depression.

FOREIGN TRADE IN FARM PRODUCTS

Farm products participated in the general increase which took place during the past fiscal year in all branches of United States foreign trade. This was true both of farm imports and farm exports, in spite of certain distorting influences that tended to enlarge the imports and diminish the exports. Chief of the abnormal forces was the persistent effect of the 1934 drought and a flight of capital into the United States from other countries. General business recovery, together with the influence of the reciprocal trade agreement program, benefited the farm export trade materially.

Exports of United States farm products rose from 669 million dollars in the fiscal year 1935 to 767 millions in 1936. Imports of farm products (including coffee, rubber, silk, and many other exotic products) rose from 971 million dollars in 1934–35 to 1,185 million dollars in 1935–36. As compared with the low points of 590 million dollars in exports and 612 million dollars in imports during 1932–33, the increases seem large, but neither the exports nor the imports of farm products were near the levels maintained from 1920 to 1929.

Substantially larger shipments of cotton, tobacco, and fresh and dried fruits were mainly responsible for the improvement in the exports. Our exports of cotton, including linters, totaled 6,702,000 (500-pound) bales, as compared with 5,328,000 bales the preceding year. Leaf-tobacco exports amounted to 417,539,000 pounds, against 353,347,000 pounds the year before. Improvement in the exports of fresh and dried fruits, practically all classes of which showed substantial gains, was in part a result of foreign duty reductions brought about under the reciprocal trade agreement program. Exports of lard, cured pork, and wheat, continued to reflect the reduction in supplies caused by the drought of 1934 and by heavy rust damage to wheat in 1935. Lard exports fell to the lowest figure in recent years. There were practically no exports of domestically produced wheat.

An important part of the increase in the agricultural imports was the so-called competitive products. It is necessary to distinguish

between products like sugar and wool, of which we regularly import a great part of our supplies, and products such as corn, wheat, and rye which we import in significant amounts only under exceptional conditions. Most of the increase after 1932 in the value of our competitive agricultural imports was in the regularly imported items, which tend to be imported in greater quantities as economic conditions improve. But some of it in the last fiscal year was in grain and feeds, meats, dairy products, and eggs, the domestic production of which had been reduced by the 1934 drought. Imports of this character reached their peak during the first quarter of the fiscal year and then declined. The 1936 drought may again increase the imports of these products.

Another important distinction exists between noncompetitive imports and imports similar to commodities produced in the United States. Our total agricultural imports in 1935 amounted to 1,073 million dollars.[1] Of this amount 483 million dollars, or 45 percent, consisted of noncompetitive items, like coffee, rubber, raw silk, bananas, spices, cocoa, and tea. There remained 590 million dollars' worth of imports similar to or capable of being directly substituted for our own agricultural products. About 134 million dollars' worth of sugar came in under strict quantitative limitations and cannot properly be deemed competitive. Subtracting the sugar leaves only 456 million dollars in competitive imports, or about 42 percent of the total of all agricultural products imported during the calendar year 1935. This total may be compared with our farm export total of 747 million dollars during the same period.

Significance of Competitive Imports

Despite the domestic shortage of certain farm products, our imports of competitive commodities were less than two-thirds as high as the annual average for the decade preceding the depression. In most cases they represented an insignificant proportion of our normal output of similar products. They fell far short of offsetting the deficits left by the drought. Imports of corn in 1935 amounted to only 1.7 percent of our average annual corn production from 1928 to 1932. Wheat imports were 3.2 percent of the average production, oat imports only 0.8 percent, barley imports 4.7 percent, pork imports 0.1 percent, and beef imports of all kinds only 3 percent.

The drought of 1934 caused a reduction of 50 million tons from our average production of feed in the United States. In the year and a half from July 1934 to December 1935, imports of feed and fodders of all types amounted to less than 3½ million tons, or only 7 percent of the shortage. Imports made up only a trifling part of the loss in production caused by the drought. The same was true of wheat, meat, and dairy products. Farmers met the feed shortage not primarily by imports, but by lighter feeding of animals, earlier and heavier pasturing, and heavy marketing for slaughter.

As a result of this year's drought we may have to import some feed. This is the logical procedure, good for both producers and consumers. Agriculture's problem is not how to stop a moderate

[1] Excluding distilled liquors.

flow of competitive imports following a crop failure but how to plan for its normal conditions, which are those of a surplus country. Normally, American agriculture encounters its major foreign competition abroad. It produces for export; and temporary shortages induced by drought should not hide the fact that an import-exclusion policy would react adversely on the export trade. Besides hurting the farmers, who must purchase feed in short-crop years, such a policy would permanently injure those who grow cotton, tobacco, wheat, hogs, and fruit.

In the balance of international payments of the United States for 1935 the increase in imports, which consisted of agricultural products brought in to relieve the drought emergency, tended to obscure the persistent unbalance between our import and export trade. As a result of these unusual temporary imports, our excess of exports was only $236,000,000. While that figure is at about the level of the balances during 1932 and 1933, it is lower than that for any other year since the World War. The apparent approach of our merchandise trade to an approximate balance, however, is illusory. It will probably be reversed as soon as we have normal crops unless the trade-agreements program greatly increases our imports of foreign industrial specialties. The largest single factor in the balance of payments for 1935 was the continuing flight of capital from Europe and elsewhere to the United States. This movement of capital tended, of course, temporarily to hide the necessity for increasing our imports.

Reciprocal Trade Agreements

Agriculture is beginning to benefit from the Reciprocal Tariff Act. During the last fiscal year the United States concluded reciprocal trade agreements with nine countries, namely, Colombia, Canada, Honduras, the Netherlands, Switzerland, Nicaragua, Guatemala, France, and Finland. It had entered previously into similar agreements with Cuba, Brazil, Belgium, Haiti, and Sweden. All 14 agreements are in effect except those with Finland and Nicaragua.

It is difficult to measure the results as yet. Most of the agreements have not been long in effect and the period covered by their operation has been one of abnormally low production in the United States. Moreover, the countries with which agreements have been concluded ordinarily take only about a quarter of our total agricultural exports. It will not be possible fully to test the reciprocal trade-agreement program until agreements have been concluded with one or more of the countries that constitute our leading foreign markets, namely, the United Kingdom, Germany, and Japan.

Foreign countries have made important concessions on United States agricultural products. The agreement with Cuba substantially reduced that country's duties on American lard, potatoes, rice, and many other products. Canada reduced its duties on cured pork and lard and on a long list of fruits and vegetables. European concessions include lower import duties and larger import quotas on a long list of commodities and are particularly helpful to our fruits. France has made important concessions as well on American tobacco, and several countries have relaxed their restrictions on imports of American lard and wheat. Cotton, our leading agricultural

export, can benefit only indirectly from the trade agreements, because the foreign countries with which tariff reductions can be obtained through such agreements do not impose serious restrictions on cotton. Most of the countries with which agreements have been concluded admit our cotton either duty-free or at low rates.

The reciprocal concessions which the United States has made help our exports by aiding foreign countries to get dollar exchange. We have made a few concessions on agricultural products. Few of them, however, were in effect during recent increase in agricultural imports. Negotiating the agreements the United States has kept two principles in mind: (1) That the import duties should not be reduced below the rates prevailing prior to the enactment of the disastrous Tariff Act of 1930; and (2) that on products of primary importance the reductions should be safeguarded either by seasonal limitations or by import quotas.

In the Cuban agreement, for example, the duties on vegetables are reduced for a limited period during which our own supplies are small. In the Canadian agreement the duty reductions on cattle, seed potatoes, and cream apply to strictly limited quantities. The only important agricultural items on which duty reductions have been made without some such safeguard are various types of cheese and imported wrapper tobacco. But the duties on cheese have not been reduced below the rate prevailing previous to the Tariff Act of 1930, and most of the types of cheese concerned are not produced commercially in this country. As for wrapper tobacco, few American farmers grow it, while many thousands produce the filler and binder tobacco which has to be combined with the imported article.

Concessions by the United States

Most of the tariff concessions made by the United States are reductions on specialized industrial items or agreements to keep on the free list noncompetitive products such as coffee, cocoa, and bananas. Other countries have made concessions to us on industrial products; and the advantage goes to American farmers as well as American manufacturers. Increased industrial exports mean more buying of farm products.

Broadly speaking, there are three types of reciprocal-trade agreements: (1) Bilateral arrangements for the exchange of exclusive concessions with individual countries, (2) arrangements based on conditional most-favored-nation treatment, and (3) arrangements based on unconditional most-favored-nation treatment. The United States has favored the third method, and it may be useful to glance at the reasons.

(1) The strictly bilateral approach is open to the objection that it would reduce our foreign trade. In our trade with most countries we export more than we import. To equalize matters with these nations individually would require a reduction in our exports. This has been the experience of European countries that have tried to achieve bilateral balances of trade. Under our present policy triangular and multiangular trading squares matters. It enables countries that buy more than they sell here to even things up by transactions with other countries which in turn may divert products to the United States.

(2) Under the second approach, the conditional most-favored-nation treatment, reciprocal concessions might be granted to countries that made equivalent concessions to us. But this method, too, tends to decrease the total trade. Few countries other than the parties to an agreement will be equally interested in the same commodities and duty reductions. Most countries will therefore be unwilling to make the equivalent concessions required. Moreover, they will object to discriminatory tariff treatment and may retaliate with higher duties against our goods.

The result may be a tariff war and new obstacles to international trade. Even without retaliatory measures discriminatory treatment under the conditional principle may force trade into more restricted channels. Changes in foreign trade affect the domestic markets.

(3) The third or unconditional most-favored-nation approach has been followed by the United States in all cases except that of Cuba, under the present trade-agreement program. This is the policy required by the Reciprocal Trade Agreements Act, which directs the Government to grant any tariff reductions to all countries except those that discriminate against the commerce of the United States. Under this last restriction Germany and Australia have been denied the benefit of most-favored-nation treatment, but all other countries receive it. The unconditional most-favored-nation treatment, which has been followed by the United States since 1922, has the great advantage of affording a guarantee of no discrimination against us in our foreign markets.

In negotiating the Brazilian agreement the United States did not get a reduction in the Brazilian duty on wheat flour. Subsequently, however, the Brazilian Government reduced its flour tariff on its own initiative. The unconditional most-favored-nation clause in our trade agreement with Brazil gave the benefit of this reduction automatically to the United States, as well as to other countries. Conversely, Germany has been unwilling to come to an unconditional most-favored-nation understanding with the United States. As a result we have lost part of our market for agricultural products in that country.

What Should We Import?

In deciding the kind of imports that we should encourage under reciprocal-trade agreements it is important to remember that the United States tariff has had its greatest effect in the past in preventing imports of industrial products, and therefore in raising the prices of the things that farmers buy. The domestic market for most industrial products is relatively elastic, whereas the domestic market for most agricultural products is relatively inelastic. Many existing tariffs merely serve to bolster industrial monopolies, which use their advantage to obtain high prices. The major markets for United States farm exports are to be found in industrial producing countries such as Great Britain, Germany, and Japan. If the trade-agreements program is to go forward successfully we must conclude agreements with the large industrial countries and offer reductions in our duties on manufactured products.

THE 1936 CROPS

The year 1936 ranks next to 1934 as the most disastrous season for crops in the history of the country. Records going back to the early 1860's include no seasons comparable with 1936 and 1934 in loss of acreage and reduction of yields. Both years brought great droughts. This year's drought reduced crop production to about one-fourth less than the usual output; whereas the drought of 1934 reduced it to about one-third less.

Geographically, there was a striking resemblance between the two droughts. They were particularly severe in the whole area stretching from North Dakota and eastern Montana to north-central Texas, and extending eastward over Missouri, southwestern Illinois, southern and western Iowa, and west-central Minnesota. Northeastern Wyoming, parts of eastern Colorado, northeastern New Mexico, and northwestern Arkansas also suffered severely in both years. In both seasons the production of wheat, corn, oats, barley, rye, and grain sorghums was greatly reduced; but in 1936, except in limited areas, there was no repetition of the acute shortage of hay and roughage that caused so much trouble in 1934.

Corn production in 1936, as a result of the drought, was slightly smaller than that of 1934 and was the smallest corn crop harvested since 1881, when our population was only 40 percent of what it is today. Of the eight States which usually produce two-thirds of the total corn crop seven had even less rainfall during the summer months than they had in 1934. The corn crop was particularly poor in the Dakotas, Nebraska, Kansas, Missouri, and Oklahoma. In these States the acreage that could be harvested for grain was largely limited to the river bottoms, to areas favored by local showers, and to irrigated sections. Much of the crop was cut early for forage and silage or was pastured by livestock. Grasshopper damage was severe in some areas and in these localities crops had little value even for fodder. Present indications are that the total corn crop is only about 1,458,000,000 bushels as compared with an average of 2,553,000,000 bushels for the period 1928 to 1932.

About one-fourth of the acreage seeded to winter wheat was a loss as a result principally of drought conditions. Scarcely more than half of the seeded spring wheat acreage was harvested for grain. The total wheat production was only about 630,000,000 bushels. This is more than was produced in any of the preceding 3 years, all of which were very unfavorable, but less than the production of any other year since 1917. Rye suffered likewise. Abnormally high temperatures and drought combined reduced oat yields in practically all the important oats-producing States except those along the Pacific coast, and in some States caused nearly a total loss of the crop. Oats production is estimated at 777,000,000 bushels, or about two-thirds of the usual production. However, it was about 43 percent greater than the very short oat crop of 1934 and slightly above the crop of 1933, though below the production in any other year since 1896. The barley crop was reduced by one-half. It is estimated at 145,000,000 bushels, as compared with 282,000,000 bushels in 1935. Production of grain sorghums is estimated at 59,000,000 bushels, as compared with 97,800,000 bushels in 1935.

The Feed-Grain Supply

Production of corn, oats, barley, and grain sorghums combined is only about 58,000,000 tons, as compared with 93,000,000 in 1935, and 54,000,000 in 1934. In other years since the World War the combined production of these grains has averaged 100,000,000 tons and has ranged from 85,000,000 to 117,000,000. Reserves of grain on land will be closely utilized and net imports of grain and feedstuffs may have to be increased somewhat; but most of the shortage will be met by feeding hogs less grain than usual.

There is a fair supply of hay and roughage. Hay production is only about 10 percent below the average. In 1935, three-fourths of the States had hay crops above the average, and the supply of old hay on farms at the beginning of the season was rather large. But many farmers had to use some of their old hay this summer. By utilizing straw, fodder, and other roughage a little more closely than usual and by using part of their reserves, farmers will be able to feed nearly the usual quantity of hay per unit of livestock.

Rice, sugar beets, and irrigated crops generally gave good yields. So did cotton and peanuts east of the Mississippi River. Tobacco, with yields about the average, was moderately light, drought having prevented expansion of the acreage. The buckwheat crop was the smallest since the Civil War. Drought damaged it severely in practically all producing States. Flaxseed production, though greater than in 1934, was below that of any other season in 60 years. Potato production was below average and sweetpotatoes about an average crop. As noted elsewhere in this report there was a fair supply of commercial vegetables and a light pack of most canning vegetables except tomatoes.

WEATHER CONDITIONS OF 1936

Weather conditions in the United States in 1936 were extremely abnormal. During the spring months they produced unprecedented floods in the Eastern States, bad dust storms in the Middle West, and destructive tornadoes in the South. Later the most severe drought of record developed in the interior States. The drought was the third in recent years, others of tremendous national significance having occurred in 1930 and 1934. This year's drought, besides causing enormous damage to crops, inflicted great hardship on farm people throughout an immense area, particularly in States that had not recovered from the drought of 1934. It aroused fears among some people that our climate might be undergoing a permanent change, though there is no scientific evidence that such is the case, and led to speculation as to whether recent conditions might possibly be due to some human activity. Various suggestions for preventing drought have been made. In general these suggestions fail to distinguish between basic changes in climate and proposals for mitigating or preventing some of its untoward effects. It will be interesting, after glancing at what the weather did to us in 1936, to notice what meteorological science has to say about the causes of floods and droughts—for both floods and drought have a common origin in the natural laws that govern evaporation and precipitation.

The floods in the Eastern States followed a severe winter, accompanied by the heaviest snowfall in many years in the country north of the Potomac, the Ohio, and the Missouri Rivers. Mild, rainy weather late in February and early in March caused rises and ice gorges in the rivers of New England and the Middle Atlantic States. About March 17 heavy rains fell on well-saturated and semifrozen soil, and the percentage of run-off was unusually high. Moreover, the northern rivers were at or above flood stage, and those in Maryland and Virginia, while not in flood, were higher than normal.

The result was disastrous floods in the James, the Potomac, the Susquehanna, the Connecticut, and the Merrimack Rivers, in some of the tributaries of the Ohio River in Pennsylvania, and in the Ohio from Pittsburgh, Pa., to below Wheeling, W. Va. The Ohio River flood gave a record crest stage of 46.0 feet at Pittsburgh on March 18. The previous high-water record was 38.7 feet on March 15, 1907. Flood damage in the Northeastern States was undoubtedly the greatest of record. Many houses were destroyed, and business was partially or completely paralyzed in many industrial areas. Losses to wage earners and retailers were heavy.

The weather of 1936 was decidedly unfavorable for agriculture over the greater portion of the United States. Precipitation in the winter and early spring was very scanty in the Southwest, where the soil became extremely dry, and severe dust storms caused much damage. In May, however, there came abnormally heavy rains, which were especially helpful to winter wheat over large areas, particularly in Kansas. Other parts of the country were less fortunate. Serious conditions developed over large areas. Dry weather in May and June brought widespread damage to early truck, hay, and pastures.

Spring Exceptionally Dry

The spring was the driest of record in many southeastern localities. Great harm resulted to early crops in considerable areas, especially from North Carolina southward and southwestward to central Alabama. The winter-wheat crop, however, was not seriously affected, principally because of May rains in the western portion of the Wheat Belt and comparatively cool weather in the eastern part. Some deterioration of the crop occurred, especially in northern districts. The spring-wheat crop and other small grains in the Northwest were severely damaged. The livestock situation became desperate. Over large areas there was neither feed nor sufficient water available. However, conditions continued favorable in the North Pacific States.

The summer was abnormally hot and dry in all Central and Northern States between the Appalachian and Rocky Mountains. July had less than 10 percent of normal rainfall in considerable areas; there was less than half of normal (usually much less) in the western part of the Ohio Valley, the Great Lakes region, the upper Mississippi Valley, and throughout the Plains from Oklahoma northward to North Dakota and Montana. The States from Oklahoma northward to North Dakota had only from 20 to 36 percent of normal; Minnesota had about 20 percent; and Iowa less than 15 percent. July 1936 was drier than July 1934 in every State from Kentucky, Missouri, and Oklahoma northward to the Canadian border.

The months of June and July combined had an average of only about one-third of normal rainfall in the Plains States and about 40 percent of normal in the western Ohio and middle Mississippi Valleys. In the interior States the 2-month period was much drier than the same 2 months during the great drought of 1934. Abnormally high temperatures aggravated the effect of the deficient moisture.

The 4 months of the growing season up to the end of July were the driest of record in the Dakotas, Minnesota, Wisconsin, Iowa, Missouri, Illinois, and Indiana, and the second driest in Ohio, Kentucky, Oklahoma, Kansas, and Montana. Of the Central and Northern States between the Appalachian and Rocky Mountains, only Michigan, Kansas, and Nebraska were drier in 1934 than this year for these 4 months.

The weather during August, for the most part, continued decidedly unfavorable throughout the central valleys, with afternoon temperatures in many places reaching 100° F. or higher nearly every day. Lower temperatures and rather frequent showers were decidedly helpful in northern sections from New England westward to the Great Plains, including considerable portions of the eastern and northern Ohio Valley and some upper Mississippi Valley sections. However, during this month the drought extended southward to Texas, Arkansas, northern Louisiana, Mississippi, and Tennessee.

THE CAUSE OF DROUGHTS

There are two basic principles in rain production—evaporation which charges the air with moisture, and condensation, which releases it. The first is important, but the latter much more so in connection with droughts. The only way rain can be produced in appreciable amounts is by the air, including the invisible vapor of water, becoming cooled on a large scale. Cooling causes condensation because warm air can hold more moisture, more water vapor, per unit volume than cool air. The capacity of air, or rather of space, for holding invisible moisture doubles with each increase of 20° F. in temperature. Thus, a cubic foot of saturated air at 80° F., if cooled down to 60° F., must lose by condensation half of its water content, which appears as cloud and rain.

Air cools when rising because it comes under less and less pressure, and therefore expands; the normal fall in temperature for an ascending column of air is 1° for each 183 feet of rise. Nature effects this method of cooling in a number of ways, usually on an immense scale. Air moves from place to place over the earth's surface in mass formation. These masses come from two main regions—polar and tropical. Those from the Poles are dense, heavy, and relatively cold; those from the Tropics are warmer and lighter.

When polar and tropical air masses meet, the tropical air, being lighter, naturally flows up over the opposing dense air, just as it would flow up a mountain side. As it ascends it expands and cools, and the water vapor is cooled enough to condense and fall as rain. Cooling the water vapor in this way is nature's method of producing rain in appreciable amounts. It is the only effective way.

When the normal courses of these opposing air masses are disrupted for a considerable period, abnormal conditions, such as

droughts, result. These processes have a world-wide relation. Nature's weather factory is the whole world, and some of its operations have not yet been discovered. Just how and why these abnormal conditions establish themselves and persist so long, meterologists have not determined. Enough is known, however, to make ridiculous any suggestions that men can basically change the order of things.

New Methods in Weather Forecasting

It has become practicable during recent years to supplement empirical methods of weather forecasting, as developed in the nineteenth century on the basis of experience alone, with rational procedures based on an understanding of the physical processes involved; and as a result, weather forecasting has for some time been developing along sound physical lines, though for a long time it must continue to be a combination of physical reasoning with methods based on accumulated practical experience with synoptic charts.

Modern contributions to the difficult problem of weather forecasting are being actively studied and tested in the meteorological services of the United States and other countries, and the Weather Bureau is keeping informed on all important developments in this field. During the fiscal year 1936 substantial progress was made in developing air-mass analyses and applying them in forecasting.

In air-mass analysis attention is primarily directed to the great streams of air that are present over a given region and are composed of masses of air of different origin, properties, and motions, separated from one another by more or less pronounced discontinuities. The analysis of the synoptic map consists of the identification and delimitation of the different air masses, the determination of their motions and physical properties, and the relations of the weather phenomena to the physical processes operating.

To develop an adequate and effective working procedure in this analysis, to articulate it with the other work of the Weather Bureau, and to amalgamate it with the accumulated knowledge and experience gained in the past, requires prolonged study and trial. The work now being carried on is designed to develop, as quickly as possible, a satisfactory and workable technique. It has continually been made of greater and greater assistance to the official forecasters, who utilize it more and more in their work.

During January 1936 Sverre Petterssen, of the Norwegian Meteorological Service, conducted a series of lectures and conferences at the central office of the Weather Bureau on the physical analysis of weather maps (by the principles of air-mass analysis and also by certain principles based on the kinematic theory of fluid motion), and on weather forecasting. The analysis of maps and the making of forecasts are two quite distinct things; and Dr. Petterssen's investigations have dealt particularly with the step from analysis to forecast. Great benefit to the work of the Weather Bureau has resulted.

In addition, a limited amount of research work on several problems involved in air-mass analysis and its practical applications has been done—particularly a preliminary study of the physical phe-

nomena leading to the development of the severe cold waves which often enter the United States from Canada.

The past 7 years have been characterized by extreme heat and widespread droughts in summer, wind and dust storms of unprecedented violence, damaging floods, and during 1935–36, extremely low winter temperatures extending over wide areas of the country. As a result of these abnormal weather conditions thousands of human lives have been lost, millions of dollars worth of property has been destroyed, and the income of many farmers has been wiped out or greatly reduced. The need for pursuing research studies looking toward the making of long-range weather and crop predictions is more apparent today than ever before. If there is one chance in a hundred of discovering the causes of abnormal weather, the effort is worth making, for agriculture, business, and the whole Nation would gain thereby.

Projects Under Bankhead-Jones Act

Under the Bankhead-Jones Research Act two lines of work have been undertaken. One, in which the Weather Bureau, the Bureau of Agricultural Economics, and meteorologists of Harvard University and the Massachusetts Institute of Technology are cooperating, is a survey and critical appraisal of methods now employed in attempts at long-range weather forecasting by foreign countries and by private individuals and agencies in this country. This survey should give a basis for research projects to be carried out during the fiscal year 1937 and thereafter. Certain statistical investigations also are being carried on concerning planetary and lunar relationships with terrestrial weather, and periodicities in weather and solar phenomena. The other study is concerned with the relationship between weather and crop yields and involves the cooperation of several bureaus of the Department, such as the Weather Bureau, the Bureau of Plant Industry, and the Bureau of Agricultural Economics, and also the assistance of a number of State agricultural experiment stations. From these preliminary studies the Department expects to develop more intensive research in crop-yield variations and weather factors during 1937 and subsequent fiscal years.

Comprehensive soil, phenological, yield, and weather data have been collected from experiment-station records in nine North Central and two Middle Atlantic States and from records of the dry-land farming stations of the Bureau of Plant Industry. Statistical technique is being developed for determining the validity of combination or segregation of yield series of different rotations, soil treatments, variety tests, etc., in order to form series that may be used in measuring crop-yield responses to fluctuations in weather phenomena. Most weather-crop research to date has been on an extensive scale geographically; averages of crop yields and weather by States and regions have been studied. It is believed the present, more intensive approach will lead to greater knowledge of the basic laws involved. A beginning has been made in the evaluation of work previously done in this field.

Under the Bankhead-Jones Research Act a project has been set up in the Bureau of Agricultural Economics in cooperation with

Harvard University to provide for the study of relationships between solar and terrestrial phenomena, especially relationships having a bearing upon long-range weather forecasting. Equipment is being designed, using the principles of telephotography, for making daily observations of the sun's corona. Heretofore measurements of this important indication of changes in solar activity have been possible only at infrequent times of complete eclipse of the sun.

In addition the Weather Bureau, with an allotment of funds from the Works Progress Administration, has continued its investigations begun with funds assigned it by the Civilian Works Administration. This work consists in computing correlations between conditions in the United States and precedent conditions in foreign countries. So far correlations have been completed between temperatures by quarters in 12 districts of the United States and pressure conditions at 60 foreign stations distributed throughout the world, both in the Northern and Southern Hemispheres. The time intervals employed were 3, 6, and 9 months. The survey of rainfall conditions in the United States as compared with precedent pressure conditions at the 60 foreign stations is rapidly nearing completion. It is planned next to compute corrrelations between foreign temperatures and foreign rainfall with subsequent temperature and rainfall conditions in the United States.

MEASURES FOR DROUGHT RELIEF

With other Government agencies both Federal and State, this Department cooperated in measures for drought relief. It so modified the soil-conservation program as to make allowance for conditions beyond the control of the farmers; issued supplementary provisions to increase the production of feed and forage; encouraged the planting of emergency forage and hay crops; and in general enabled farmers in drought areas to take advantage of the income-insurance features of the program. The Government's readiness to make purchases of livestock from drought areas protected markets against sharp declines. Loans for the purchase and storage of seed enabled farmers to prepare for the next crop. An agency established at Kansas City facilitated the movement of feed into drought-stricken areas and also the movement of livestock from drought areas to localities where surplus feed and pastures were available.

Under the surplus-removal clauses (sec. 32) of the amended Agricultural Adjustment Act, quantities of food and feed became available for relief in drought States. Between June and September the shipments included 1,171 carloads of foodstuffs for human consumption and 375 carloads of millfeed for livestock. Some shipments of this kind would have been made in any case; but the drought emergency necessitated a considerable increase in shipments to drought areas. The Resettlement Administration made loans and grants to farmers for the purchase of feed, seed, forage, and food; the Works Progress Administration provided employment to farmers in road construction, in well digging, and in building small dams and reservoirs. The Farm Credit Administration alleviated credit difficulties, and the Federal Surplus Commodities Corporation carried

out a small-grain seed-conservation program. Western and Middle West carriers reduced freight rates on feed and livestock.

Beef-cattle numbers were more nearly in balance with feed supplies and with market requirements than they had been during the drought of 1934. Indications were that prices would be favorable to producers in 1937. There was no need, as there had been in the previous emergency, for the Government to buy several million head of cattle. It purchased only enough to prevent sharp price declines, and restricted the purchases to the classes and grades of cattle least suitable for resale as stockers and feeders and least desirable for breeding herds. It disturbed the commercial cattle trade as little as possible and encouraged a movement back to the country for feeding and breeding.

The A. A. A. began purchasing cattle in the drought area on August 3, when market receipts above normal requirements caused a decline of prices. It made limited open-market purchases at terminal markets serving the drought territory. Up to September 4, however, it had purchased only 2,964 head. By that time fall rains in parts of the drought territory had encouraged farmers to retain cattle and had increased the demand for feeder stock. Funds available under section 32 of the amended Agricultural Adjustment Act provided the means for purchases of surplus livestock. The payments to farmers and ranchers were purchase payments only; they did not include additional benefit payments, as the cattle and sheep purchases in 1934 had done. Meat resulting from the buying programs went to the Federal Surplus Commodities Corporation for relief distribution.

Seed-Grain Situation

There was a shortage of small grains suitable for seeding in the drought territory. The seed-grain purchase program helped to prevent an acute deficiency and to obviate the planting of light and undesirable seed in 1937. It provided for an advance of not more than $10,000,000 to the Farmers' National Grain Corporation, a farmers' cooperative, for the purchase of between 7,000,000 and 9,000,000 bushels of spring wheat, durum wheat, oats, barley, and flax. Seed grain thus acquired will be sold to farmers at reasonable prices before seeding time in 1937. Supervised by the Federal Surplus Commodities Corporation, the seed-purchase program included efforts to conserve and store desirable seed stocks.

It became evident in September that little corn suitable for seed in the western and north-central part of the Corn Belt will be available for the year's crop. Reports from large sections of the western Corn Belt indicated it would be necessary to get from 2,000,000 to 3,000,000 bushels from other localities outside the worst drought-stricken sections. As a means of guarding against a shortage of adaptable varieties, the Government offered two types of non-recourse loans on farm-stored seed corn. One type made available a loan of $1.75 a bushel on field-selected corn having proper germination and storage qualities. The other offered a loan of $0.55 a bushel on good quality and properly stored crib corn, suitable for sorting at a later date. Each loan note gave the Government a purchase option

amounting to $3.50 per bushel on the field selected and $1.50 a bushel on crib-selected corn, shelled and graded in the sack.

It proved difficult for the railroads to grant blanket reductions in freight rates on shipments of feed and livestock. They feared to incur some liability for discrimination, against which they had been specially protected in 1934 by a provision in the Drought Relief Appropriation Act. However, they made piecemeal concessions. In the most seriously affected areas carriers quoted emergency rates on hay amounting to two-thirds of the normal rates. On coarse roughages they quoted 50 percent of the usual hay rates. On coarse grains and feeds and on feed ingredients they accepted shipments at two-thirds of the normal rates. These concessions enabled farmers to obtain feed from distant points and helped to keep local feed prices at more reasonable levels. On shipments of livestock to surplus-feed and pasture areas the railroads made a rate of 85 percent of the normal rate, with the privilege of returning the cattle on a 15-percent basis.

Comparison With 1935 Feed Supply

The production of feed grains as estimated on September 1, 1936, was approximately 42 percent below the average for the 5 years, 1928 to 1932. But the number of livestock on farms was slightly less than during the 1928–32 period. In consequence, the production of feed grains per grain-consuming animal unit was only about 38 percent below the 1928–32 level. In terms of feed-grain production per animal unit, the output was about the same as that of 1934. The 1936 drought came later than that of 1934 and covered a smaller portion of the range and pasture areas of the West. Early hay production was not so seriously affected. Hay production per hay-consuming animal was only about 14 percent below the 1928–32 average, as compared with 35 percent below in 1934. Because the 1934 drought became serious early in the season, Congress appropriated $525,000,000 for drought-relief activities. This year's drought did not become serious over large areas until late in June. No special appropriation for meeting it had been provided. Federal and State agencies modified their programs, however, in such a way as to provide substantial assistance to farmers in the drought areas.

LONG-TERM POLICIES FOR DROUGHT AREAS

Looking toward the development of a long-term program calculated to render future droughts less disastrous in the Great Plains region, a committee appointed by Executive order visited the region, conferred with farmers and public officials in the areas most seriously affected, and drew up a series of recommendations. The committee utilized the experience of numerous Federal and State agencies, many of which had dealt for many years with the problems of the semiarid lands. These agencies placed a mass of material at the committee's disposal, and the conclusions reached were in large part the result of studies and experiments begun long ago. In thus bringing to a focus the best available knowledge on the subject the committee accomplished a work of outstanding public importance and laid a foundation for an effective remedial policy. The com-

mittee's findings, in which I heartily concur, may usefully be summarized in this report.

Analyzing the causes of the present disaster, the committee assigned primary importance to the attempt which has been made for several decades to impose on the Great Plains a system of agriculture not adapted to the region. Methods suited on the whole only to a humid region were introduced into a semiarid region. This was largely the outcome of a mistaken public policy. The Federal homestead law, for example, kept land allotments low and required that a portion of each allotment should be plowed. This policy, the committee said, caused immeasurable harm. On the western Plains it was both a stimulus to overcultivation and a condemnation of the cultivators to poverty.

Efforts to cure the trouble by enlarging the allowable individual holding did not work. In western North Dakota and Montana tracts two or three times the size of those actually granted would have been necessary to support farm families adequately. As the ranges were enclosed, feed crops were grown by intensive cultivation and the ranges were overstocked. Overcropping, overgrazing, and improper farm methods generally made the soil loose and unstable, promoted soil blowing and washing, lowered the ground-water level, and rendered the whole area extremely vulnerable to periodic droughts. The settlers themselves could not avoid these mistakes. They lacked both the knowledge and the incentive to do so and were the victims of a mistaken national policy.

Settlement of the western Plains began, the committee observes, at the end of what appears to have been a 40-year dry period. It proceeded during a wet period which now seems to be terminated. Droughts in the region during the latter part of the nineteenth century and the early years of the twentieth century were brief and infrequent. Farmers regarded them as exceptional and did not change their farming methods. Weather records indicate, however, that a long dry period preceded the settlement of the Great Plains and that we may now be in the midst of another prolonged dry period. This may have its wet years but may keep the average rainfall for a period below the long-time average.

It is impossible to make a confident forecast. But whether the present drought condition be brief or prolonged, the problems of the Great Plains region will remain essentially the same. Continued farming and ranching by the existing methods will cause continued trouble under any climatic conditions that are likely to prevail. The problem is not the product of a single drought or even of a series of bad years. It is the outgrowth of a mistaken policy pursued for decades.

The Critical Area

The Great Plains comprise an area stretching from west central Texas to the border of Canada. On the west the Rocky Mountains are the border. On the east the region is irregularly delimited near the one-hundredth meridian, where formerly the short-grass country merged into the tall-grass or prairie country. In the critical area are the Texas Panhandle, the Oklahoma Panhandle, northeastern New

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Mexico, and all the northern portion of the Plains. Annual rainfall is low throughout the entire region. There are short, intense storms, wide fluctuations of temperature, and strong prevailing winds. Frost and snow make wind erosion a less serious danger in the north than in the south; but soil blowing and soil depletion occur throughout the region, particularly in areas of excessive plowing.

Millions of acres of the natural cover, the buffalo grass and grama grass, have been destroyed in the Great Plains and the soil made loose by continued cultivation, decay of grass roots, and reduction of the humus supply. This destructive process has been accelerated since the World War. Eight States lying partly within the region had 103,200,000 acres of harvested crops in 1929, as compared with 87,800,000 in 1919 and 12,200,000 in 1879. How wrong this plow-up program was can be inferred from the records made under the Homestead Act. Only 60 percent of the entries were perfected prior to 1916. Since then only 45 percent of the entries have been perfected.

The results of attempts at the intensive cultivation of the Great Plains over a tremendous aggregate area have been bankruptcy, tax delinquency, absentee ownership, and excessive tenancy. In 1935 the percentage of tenant farmers in eight Great Plains States was 41.1, as compared with 15.5 in 1880. Many farms have been abandoned. Many residents moved out of the Great Plains between 1930 and 1935. The "suitcase farmer", of whom there were too many, visited his land only a few weeks each year for planting and harvesting. In drought years he abandoned his crop. He never made permanent farm improvements. Community services declined. The problem is not simply one of short-term relief but of long-term readjustment and reorganization.

Primarily, it is necessary to check overcropping and overgrazing, so that both soil and water may be conserved, and this end cannot be attained exclusively by individual action. Yet the committee's proposals do not strike at the independence of the individual farmer. On the contrary, the action recommended should restore an independence that has largely been lost. New public policies, designed to correct the existing mistaken policies, will stabilize the economy of the region and increase its power to maintain independent farm families. The fundamental requirement is to bring farming and livestock-raising methods into conformity with the natural conditions.

In many measures the Federal Government should take the initiative, particularly in leadership and guidance. Federal participation may be necessary also in the construction or financing of public works. Past Federal policy encouraged the misuse of the Great Plains. Present Federal policy should encourage the correct use. In emphasizing this principle the committee states that there need not be any conflict of jurisdiction between Federal agencies on the one hand and State and local agencies on the other. It believes that joint cooperative effort will prove workable, and more effective than any other method. Needless to say, the action taken should be continuous over a long period, with Federal and State agencies undertaking the functions they are best able to perform.

Combination of Measures Necessary

Efforts to develop a Great Plains economy capable of withstanding recurrent drought will require various measures involving Federal, State, and local cooperation. The basic aim should be to arrest excessive soil erosion and to conserve water. Public grants and subsidies should be harmonized with a plan calculated ultimately to do away with the need for such aids.

Soil and water conservation will require engineering, good agronomy, changes in tillage practices, financing, and public education. On cultivated land it will be necessary to promote contour plowing, listing, terracing, strip cropping, and other soil-conserving practices. Dams may be of use in checking water erosion and in holding water for use in dry periods. Reservoirs and wells should be developed. Small irrigation systems for groups of families will be found useful. In some areas large irrigation projects may be needed. Certain submarginal lands should be permanently withdrawn from farming.

Measures of this kind, however, can merely improve the conditions and practices on individual farms. They cannot effect the basic changes necessary in the whole land-use pattern. Therefore the committee recommended that public acquisition of lands should be continued on the basis of selecting those areas less suited to cultivation and grazing. Extension of the grazing range could be brought about in certain areas by bringing some arable farm land under public ownership. Abandoned farms or tax-delinquent land could sometimes be acquired. Land in some areas, it proposed, should be leased or optioned, with a stipulation that the users shall carry on an approved program of restoration to grass or forest.

Public land buying and regulated grazing, however, will not be fully efficacious if private owners may still use their holdings in a manner destructive to neighboring property as well as to their own. Therefore the committee suggests that the possibility of restraining wrong land uses should be explored within legal and constitutional limits.

In some areas cooperative grazing districts are attempting to prevent the overgrazing of their lands; and this policy the committee warmly endorsed. Each thing done, it declared, should be part of a coordinated project covering the entire region. As an aid to the cooperative control of grazing, it suggested that public land buying in some areas would help to block out desirable ranges. Such a project could be set going without arbitrary action by any public agency, and it could be carried out democratically by using existing facilities for ascertaining local interests and wishes. The pooling of scientific knowledge in a well-conceived educational campaign would be indispensable.

Research should be undertaken to determine how many people the region can properly support. With that determined, the problems of migration and relocation would be simplified. While discouraging aimless migration, the committee believes that in some areas a regrouping of the population would be beneficial. It is impossible, as yet, to determine whether or not the region can adequately support its present population. A shift from cropping to grazing might reduce the population in some localities but at the same time increase

the real wealth of the region as a whole. Ultimately, the change would provide additional income. The fundamental purpose is not to depopulate the region, but to make it permanently habitable. Any other aim would be a confession of failure. In the long run the Great Plains will support more people on a higher standard of living if its agriculture is regulated intelligently than it can possibly support if present tendencies run their course.

In some localities farm holdings should generally be larger than those now prevailing. Such necessary increase in the size of farms would require governmental assistance. State and county governments may expedite the consolidation of small units by making available to grazing and other cooperative agencies certain tax-delinquent lands, which will not again be cultivated by their nominal owners. The aim should be to develop holdings large enough to support farm families in independence and comfort.

It is proposed that the possibilities of rural zoning be explained as a means of preventing the sporadic settlement and breaking up of lands better adapted to range use than to arable farming.

The committee recommends the use of public credit to enable competent tenants to purchase and operate their own farms. Tenancy, it says, promotes soil mining and does not suit the Great Plains. Also, the committee recommends the study of crop insurance and of ways and means to promote the transfer of certain croplands to grass farming. It urges public guidance in resettlement, and investigations to determine what new Federal legislation, if any, will be necessary. Essentially the committee finds that, while present methods in the Great Plains do not promise success, methods suited to the region can be developed through Federal, State, and local cooperation.

Crop Insurance

In the farmer's life luck and chance are important factors. Each crop planted is a speculative venture. Unfavorable weather conditions, floods, insects, or disease may cause a partial or a complete failure of his crop. Studies of total farm income for all farmers do not tell the whole truth. Increases in prices in years of low production enhance the income of farmers who have a good crop, but benefit very little those whose crop fails. The distress due to widespread crop failure and the resulting necessary expense for relief suggest the need of some form of crop insurance.

The programs of the Agricultural Adjustment Administration contained a measure of crop insurance. The benefit payments were the only income of many farmers after the drought of 1934 had destroyed their crops. Undoubtedly the soil-conservation payments of 1936 will likewise serve as crop insurance in drought areas. Crop insurance resulted as a byproduct of the adjustment program in connection with the administration of the Bankhead Cotton Control Act. In 1934 many farmers in the western part of the Cotton Belt produced less cotton than their allotment of tax-exemption certificates covered. Through the operations of a pool set up to make transfers, they were able to sell their surplus certificates to farmers elsewhere who had produced cotton in excess of their allotments. Sale of their certificates

enabled farmers who had suffered a partial or complete crop failure to recoup part of their losses.

The principle of crop insurance merits a prominent place in any broad plan for a national farm policy. Insurance viewed from the standpoint of the individual appears primarily as a contract for the indemnification of losses. Viewed from the standpoint of the whole group, however, it appears rather as an averaging of losses. The insured individual pays the average loss instead of taking the chances of suffering a larger loss. Insurance is a social device by which "the loss lighteth lightly upon the many rather than heavily on the few."

Crop insurance is a means by which systematic contributions by farmers, made in proportion to the risk to their crops, create a reserve out of which agriculture can finance its own relief from crop disaster. It does not prevent disaster, but it does provide that the full weight shall not fall on a few.

Crop insurance differs in some respects from other types of insurance. It insures against the loss, not of an existing value, but of a prospective value. In fire insurance loss can readily be measured, because the value of the property is known or can be estimated. But if a crop fails, what is the loss? Is it the difference between the actual production and a bumper crop; between the actual production and an average crop; or between the actual production and the investment in the crop?

Many have questioned whether it is sound policy to insure prospective profits and have advocated insuring only the investment in the crop. But the investment in the crop is difficult to determine. Much of it represents the farmer's labor and other items that must be evaluated. Little of it represents a cash outlay that can be measured accurately. It seems better to insure only a certain proportion of the average yield. That is much simpler. If only a reasonable percentage of the average yield is insured, the plan does not include the insurance of prospective profits.

Requirements of Crop Insurance

Crop insurance should have a large element of saving. That is, it should involve not merely a horizontal averaging of losses for each year but also a vertical averaging of losses over a period of years. Losses in certain years may be so widespread that accumulations from more successful years are necessary to help carry the burden. This is very important. Hence the rates for crop insurance should be based on the average losses over a long period or over a shorter period that was worse than the average for most short periods of years. The successful operation of a plan for a few average years does not prove that it could successfully meet widespread disaster for several years. Substantial reserves should be built up in good years.

All-risk crop insurance is not available to the farmer today. Insurance companies have made several attempts to insure the crop of wheat and other grains. In 1917 such an attempt in the spring-wheat area failed partly because of drought and partly because insurance was written after it became apparent that there would be a short crop. In 1920 another attempt failed largely because it included price insurance, and prices fell off sharply. Still another attempt in 1931 and

1932 failed because of a sharp drop in prices. But hail insurance, a specialized type, has proved successful.

Insurance has quite frequently been written on fruit and vegetable crops, particularly against frost and freeze hazards. Such insurance has sometimes been taken out only to protect the creditor. There is little being written today, most of the companies having withdrawn from the field. The experience was not always successful. The hazards were so great that a single company could not afford to carry the risk and reinsurance on such business was difficult to arrange. The large uncertain hazard for a single company necessitated high rates.

If crop insurance is to be made generally available to the farmer, probably the Government must assist. The Government is better able than private enterprise to carry out the venture on a scale large enough to reduce the impact of heavy losses in certain areas. Insurance, where extensive public protection is at stake, is not new for the Federal Government. We have insurance of bank deposits, insurance of loans for financing the construction and repair of houses, and life insurance for veterans. Also, we have unemployment insurance and a system akin to insurance for providing old-age annuities. Crop insurance would provide the farmer with a measure of social security comparable in some ways to the unemployment insurance and old-age retirement from which he is excluded under the Social Security Act.

Crop insurance, to be successful, should have an actuarial basis. There is little crop-insurance experience to study and reliance must be placed on the loss experience of farmers in general, with proper allowances for an adverse selection of risks. This Department is studying the problem with data for individual farms gathered incident to the adjustment programs of the Agricultural Adjustment Administration. These data cover a 5- to 6-year period which included several drought years. They are supplemented by estimated average-yield data for a long period. The estimates of cost derived therefrom should be conservative. The study emphasizes a type of insurance in which the coverage would be a certain fraction of the yield on the insured farm. Such a plan would not put a premium on the farming of poor land or on poor farming practices.

Differences among areas and counties are being studied, because rates would have to vary. Rates based on average costs over a wide area would attract only those who were favored by these rates. They would bring into the insurance group only farmers with risks greater than the average. In that event the losses would exceed the premiums collected. As far as possible, premium rates and insurance coverage should be so adjusted that each type of farmer and each type of farm would bear its own cost. Over a period sufficiently long, each farm should bear its own cost.

Crop insurance must not benefit the shiftless at the expense of the thrifty, and the poor land at the expense of the good. In large measure the insurance coverage and the premium rate should be based on the experience of the individual farm. The insurance coverage for an individual farm should probably be a given percentage of the average yield for that farm. The premium rate should prob-

ably, in a measure, be based on the average crop losses of that farm. The data acquired for individual farms in the agricultural-adjustment program might provide a starting point.

Principle of the Ever-Normal Granary

Crop insurance would be an attempt to solve the problem of short crops. But bumper crops have not been an unmitigated blessing to the farmer. Frequently a large crop sells for less than a medium or a small crop. Both problems arise from wide variations in production, the one being the counterpart of the other. Perhaps a single solution could be worked out for both problems. Some system that would tend to level off the amount that individual farmers could and would place on the market in various years would tend to solve both problems.

In line with this thought the Department, in its studies of the costs of crop insurance, has given some consideration to the possibilities of the option of paying for the insurance "in kind", out of the production of years of surplus. This should make the burden of the insurance premiums lighter and easier to bear. In the sample studies that have been made the surplus production was calculated for each farm, the surplus production per acre being considered as the excess of the actual yield over the average yield. Only a fraction of that surplus would be needed to pay for insuring the yields up to 75 percent of the average yield for each insured farm. In fact, for the 6-year period 1930–35 only from one-third to two-thirds of the surplus production would be necessary to meet the net cost of such insurance.

The plan, involving payments in kind and payment of premiums only in years of surplus, would really become the ever-normal granary plan with crop-insurance requirements serving as an automatic regulator. In years of surplus a part of the crop would be drawn off the market and put into storage—the amount so drawn off being regulated by the predetermined insurance rates based on actuarial calculations. In years of crop failures the stored commodities would be released, the amount being automatically determined by the amount of indemnities necessary as defined by the insurance contracts. Since the plan would operate automatically, with the commodities being released from storage only in case of crop failure, the commodities in storage would not be a potential supply on the market tending to depress the price.

During surplus years the removal of the excess commodities from the market would tend to support the price. The part of the crop not used for insurance premiums would still be more than the farmer's average production, and with a supported price the income from the crop should be reduced but little, if at all. The release of commodities from storage in years of crop failure would tend to hold down the price, but farmers without a crop do not benefit from high prices. Under this plan the farmers who lost their crop would be indemnified, while the farmers who produced a crop would get at least average prices.

Furthermore, as a form of price stabilization this plan would require no funds to buy up the commodity. The participating farmers would provide the capital in the form of premium payment in kind.

Any Plan Should Be Optional

While the above plan for crop insurance has many excellent features, it would present many problems. The Department is committed to no single plan. It is interested in all possible angles of the problem and in various possible plans. Certain plans may be suited to some areas, and other plans to other areas. Any plan adopted should be voluntary and optional with the farmer.

Crop insurance is needed most in the single-crop areas. In regions of diversified farming the loss of a single crop is less calamitous. But though diversification is a form of self-insurance, it does not adequately offset losses from extensive droughts, floods, and infestations. Another form of self-insurance is the accumulation of reserves of feed and supplies and the accumulation of savings in some form of investment. But this method, too, needs often to be supplemented.

Farmers have learned much in recent years about handling their local farm problems. Their experience under the A. A. A. should provide a base for the local administration of an insurance program. But if crop insurance is tried, it should be as an experiment and should be confined at first to one or two crops—wheat and possibly corn or cotton. It should be limited in the beginning to areas where there is a real need and a real demand. It should not be considered a complete protective program in itself, but should be part of a larger unified program involving soil conservation, retirement from farm uses of land unsuited to agriculture, judicious commodity loans, and the ever-normal granary.

COTTON

In some respects the cotton situation is better now than it has been for several years. This year's crop of 12,400,000 bales (November estimate) is larger than that of 1934 to 1935, but the carry-over of American cotton is the smallest since 1930, and the world supply of American cotton is the smallest in 12 years. There is no shortage of American cotton. On the contrary the supply is more than ample, but in comparison with the situation in recent years the present supply-and-demand relationship is not so unfavorable to the producer. In fact, returns to domestic growers promise to exceed those received for any crop since 1929.

Since August 1932 the world carry-over of American cotton has been reduced from 13,000,000 to 7,000,000 bales. Though still somewhat larger than an average carry-over, this quantity is 2,000,000 bales below the carry-over in August 1935 and is the smallest in 6 years. The total world supply of American cotton this season will be about ¼ million bales less than in the previous season, despite the increase in the 1936 crop.

Income to farmers for cotton marketed during the present crop year will probably be the largest since 1929–30, though about 30 percent below the average for the period 1919 to 1929. Among the causes of the improvement are of course recovery of business at home and abroad, changes in the supply position, and the reciprocal trade agreements program which the Government has instituted. This program benefits cotton exporters by enabling foreign

buyers to get dollar exchange. Part of the advance which has taken place in the price of cotton since 1933 may be attributed to dollar revaluation. Production control has been an important factor. The revaluation by itself would probably have encouraged farmers to increase their output and would have tended to counteract the influence of the monetary policy. The improvement in the cotton situation is the outgrowth of numerous factors the separate influence of which cannot be accurately measured.

Certain unfavorable aspects of the situation should be noticed. World consumption of cotton in the 1935–36 season was about 27,700,000 bales, the largest consumption on record. American cotton accounted for 12,500,000 bales, as compared with 11,300,000 bales the previous season. Though American cotton represented a slightly larger proportion of the consumption in 1935–36 than it did in 1934–35, it was materially below the average for the decade ended 1933. Mill consumption of foreign cotton, on the other hand, increased to a new high level and was above the 10-year average and above the consumption of American.

Numerous factors contributed to this shift in the relative consumption of American and foreign cotton, some of them of long standing. The production of cotton in other countries increased rapidly after the World War, side by side with an increase in our own production. Meantime trade restrictions throughout the world, among which our own tariff policy exercised a large influence, tended to handicap our cotton-export trade. Foreign countries turned as much as possible to foreign cottons, particularly when they could offer industrial commodities in exchange. They wanted to buy where they could sell, and the American tariff policy made it difficult for them to do so in the United States.

Obstacles to Cotton-Export Trade

When cotton prices and income fell to the low levels of 1932, it was evident that something had to be done to help American growers. With the aid of the Federal Government domestic producers undertook to readjust their output. The ensuing price recovery inevitably benefited foreign as well as American cotton growers, and the trend toward relatively increased production of foreign growths, which had long been in evidence, continued, although perhaps not to the extent implied in the trade press.

Obstacles quite independent of our production policy stand in the way of increased foreign consumption of American cotton: (1) The difficulty foreign consumers still have in getting dollar exchange, and so long as we bar out foreign goods this difficulty cannot greatly diminish. (2) Other countries are forging ahead in cotton production. (3) The competition of other fibers is growing. These obstacles, however, can be surmounted. Recent trends in our tariff policy are steps in the right direction. Our advantages in cotton growing are substantial, and the world demand for cotton should continue to increase. When he can do so without losing money, the American grower will respond. The Department is engaged in an extended cotton-breeding program which should play its part eventually in making the American cotton grower the most efficient in the world.

WHEAT

DESPITE the effects of the drought the total supply of wheat in the United States for the 1936–37 season is large enough for the usual domestic requirements. Supplies of hard red spring wheat and durum wheat are short, however, and imports of these types will continue. The drought reached its greatest intensity in the hard red spring and durum wheat areas. The winter-wheat crop was larger than that of 1935 and of good quality. Probably the spring-wheat mills will use a larger percentage of hard red winter wheat and Pacific Northwest wheat this year than they did last. More than the usual quantity of soft red winter wheat will probably be used in bread flour. It is expected therefore that the imports of milling wheat in 1936–37 will not exceed the 26,000,000 bushels imported in 1935–36.

The Pacific Northwest, the principal white-wheat region, again produced a surplus. In 1933–34 the disposal of its surplus was financed out of processing-tax funds. In 1935–36 exporters in the Pacific Northwest were indemnified for losses sustained on exports to the Philippine Islands, funds for which were made available from tariff revenues under section 32 of the amended Agricultural Adjustment Act. In this same year, as well as in 1936, considerable amounts of white wheat from the Pacific Northwest moved east of the Rockies, some of it going into relief channels. Ordinarily, however, wheat from the Pacific Northwest cannot compete east of the Rockies with Great Plains wheat, which normally constitutes the bulk of our supply of bread wheats. In years of average United States production the Pacific Northwest must seek a market abroad.

Since 1933 wheat prices in the United States have been high in relation to the world market price. They have ranged from 20 to 30 cents a bushel higher than they would probably have done had our production been normal. Average or above-average yields in this country next year would give an export surplus and cause an adjustment of the domestic price toward an export basis. On an acreage equal to that seeded for the 1936 crop, yields one-fourth below the average would provide enough wheat for the usual domestic utilization.

Our wheat farmers continue to expand their acreage. The area seeded for the 1936 crop was 74,500,000 acres, the largest on record with the exception of that seeded in 1919. In 1935 growers who had signed the A. A. A. wheat-adjustment contract had the right to plant 95 percent of their base acreage. But many had seeded winter wheat in the fall of 1935, before the contract was offered to them, and there was a tendency for farmers to plant larger acreages. In addition, nonsigners increased their seedings. Large acreage does not always mean large production. In years of normal growing weather, however, the existing wheat acreage in the United States will produce large export surpluses, for which satisfactory outlets do not now exist.

It is better to have a balanced acreage. With a balanced acreage less land shows a loss in drought years, and less wheat has to be sold below cost in years of normal crops. In 1936 the soil-conservation program provided payments to wheat growers for the diversion

of land from soil-depleting to soil-conserving crops. However, the list of soil-depleting crops included many crops besides wheat, and participating growers did not have to make any adjustment in their wheat acreage if they were in a position to divert other land from soil-depleting to soil-conserving uses.

Cash farm income from wheat in 1936 may be between $425,000,000 and $465,000,000, exclusive of payments to wheat farmers under the agricultural conservation program. The corresponding figure for 1935 was $353,284,000, excluding the $115,368,000 in the A. A. A. adjustment payments. Cash farm income from wheat in 1932 was only $195,860,000. Needless to say, the income from wheat this year will be very unequally distributed as a result of the drought. Growers in the States worst affected will receive comparatively little, while growers in the States not affected will make large returns. This rough estimate of wheat income rests partly on the expectation that world wheat prices in 1936–37 will be materially higher than they were in 1935–36. Several important wheat countries, as well as the United States, have below-average production this year.

Distribution Within the United States

Market outlets will have more effect on the distribution of wheat within the United States in the future than they have exercised heretofore. In the 1920's there was a good demand for wheat in the markets of the world. All that was grown was sold at prices fairly remunerative. That is no longer the case. Formerly this country exported principally hard red winter, durum, and soft white wheats; there was a sufficient market at home for all or nearly all our hard red spring and soft red wheats. Hereafter the absence of an adequate foreign demand may create new problems of internal competition.

Our high-quality hard wheat is produced in the Great Plains under changing weather conditions and with widely fluctuating yields. Other regions are not adapted to producing it. Varieties of hard red spring and hard red winter wheat are grown to some extent in the Pacific Northwest and in the Corn Belt, but the product is less desirable for milling than the wheat grown in the western Great Plains. Farmers in the soft red winter wheat region may shift from wheat to other crops, as the prices of the latter crops rise in relation to wheat prices. In the Pacific Northwest, however, the farmers have fewer alternative crops to which they may turn, and this region will continue to be a specialized wheat region. This area will continue to have a considerable surplus of the soft wheats for export.

In the Great Plains the bread wheats will be the mainstay. Part of the area plowed during the 1920's is better suited to ranching. Elsewhere, however, the Great Plains will continue to produce wheat, despite the prevailing climatic and other hazards, because the wheat grown there has exceptional value for milling and because wheat in large areas of the Great Plains had a marked comparative advantage over other crops. Measures should be taken to stabilize the income from wheat in this region so that the Nation may have a reasonably dependable supply of bread wheat.

LIVESTOCK AND FEEDS

Recovery in livestock production was under way last year following the 1934 drought, but this year's drought checked it. On January 1, 1936, the number of grain-consuming animal units on farms was somewhat greater than it had been a year earlier, when it was the lowest since early in the present century. On the other hand, the number of hay-consuming animal units on farms was slightly lower than a year ago, though above the 10-year (1925–34) average. In January 1937 the number of both grain- and hay-consuming animal units on farms may be as low as, or even lower than it was, in January 1935. There was relatively heavy marketing of cattle and hogs in the fall of 1936, and close culling of dairy herds and poultry flocks. Moreover, the fall pig crop was smaller than that of 1935.

Total feed-grain production in 1936 was larger than that of 1934. There was a larger supply of hay and roughage. In consequence the feed situation following the 1936 drought will be easier than was that following the 1934 drought. Farmers will be better able to winter their cattle, sheep, and work stock. But supplies of pork and the better grades of beef will be reduced next year. They may be almost as small as in 1935.

In 1936, for the third consecutive year, the demand for meats improved. Though lower than in the 5-year period prior to 1931, it was about equal in the first half of 1936 to what it was in the first half of 1931. Consumers spent for meat in this period about 12 percent more than in the corresponding period of 1935. They spent about 50 percent more than in the first half of 1933. The improvement, of course, reflected general economic recovery. There was a marked increase in both the total live and dressed weights of animals slaughtered under Federal inspection; the second half of the year will probably record a further increase. Total slaughter for the year will be much larger than it was in 1935, though less than the average for the 5-year period 1930–34. In 1937, however, both the number and weight of the animals slaughtered will decrease. It is not probable that total yearly slaughter will again be equal to the average of 1930–34 before 1940. The feed situation will affect the trend of hog numbers more than the trend of any other species of livestock.

Indications on September 1 were that the 1936 corn crop would be slightly smaller than that in 1934 and the smallest in 55 years. On the other hand, the production of oats, barley, and grain sorghums was large enough to give a combined production of feed grains of approximately 58,000,000 tons, as compared with 54,000,000 tons in 1934 and 93,000,000 tons in 1935. Corn prices will be relatively higher during most of 1937, and hog production will be sharply curtailed. Though the number of hogs available for slaughter in the 1936–37 marketing year will be larger than in 1935–36, hog production for the calendar year 1937 will be smaller than in 1936. Hog prices for the marketing year beginning October 1 will probably average about the same as they did in 1935–36.

Despite the drought, the income to corn and hog producers was materially larger than that of 3 years ago. During the winter of 1932–33 the farm price of hogs fell below $3 per 100 pounds, the

lowest level in more than 50 years. Income from the sale of hogs in 1932 amounted to only about $440,000,000, as compared with an income of about a billion dollars for a number of years prior to 1930. In 1936 the income from the sale of hogs was about $840,000,000, and the farm price averaged $8.80 per 100 pounds. This sharp increase in prices and income from the depression level in 1932 occurred despite the absence of any material improvement in foreign demand for hog products. The foreign market for United States hog products retains only a fraction of its former proportions. Import restrictions in foreign countries and a marked revival in European hog production, which began effectively to curtail United States exports of hog products a number of years prior to 1932, continue to be the principal causes of greatly reduced exports. Exports of pork and lard fell from about 2,000,000,000 pounds in the early post-war years, to a little more than one-third as much in 1932, and since have remained at approximately that level.

Uneven Distribution of Corn-Hog Income

Although the income of farmers in the Corn Belt States was much greater in 1936 than in recent years, its distribution was very abnormal. In the States hardest hit by drought, such as South Dakota, Nebraska, and Missouri, the supply of corn, hogs, and other farm products for sale was very small, and even though prices were very favorable the income of farmers was small as compared with the income in the other Corn Belt States, where the effects of the drought were not nearly so great. The uneven effects of the drought were reflected in uneven distribution of farm income. In such States as Nebraska and South Dakota, where farmers had not recovered from the effects of the 1934 drought and where very little was obtained from the sale of cash crops in 1936, the payments received for participation in the 1936 agricultural-conservation program constituted a substantial proportion of their total income for the year. As was the case in 1934, payments for participation in the agricultural program received by farmers in the drought areas were in the nature of partial insurance against reduction in incomes resulting from drought.

Cattle

The general cattle situation was less influenced by drought in 1936 than in 1934. In parts of the northern Great Plains, however, heavy liquidation of cattle was necessary. Beef cattle numbers at the beginning of 1937 will probably be smaller than they were at the beginning of 1936, though still above the average for the 10 years 1925–34. In January 1936 the total number of beef cattle, including calves on farms, was approximately 32,300,000 head, as compared with 36,100,000 head in 1934, when beef-cattle production was nearing a peak in the typical production cycle. Because of the reduced level of hog supplies, in competition for the consumers' meat dollar, the cattle industry is now in a rather favorable position, and for the next few years the trend in cattle numbers will probably be upward. In the first half of 1936 the average price paid by packers for all cattle slaughtered under Federal inspection was $6.60 per 100 pounds, or slightly lower than that in the first half of 1935.

Sheep

Sheep and lamb producers fared comparatively well during the last months of 1935 and most of 1936. Prices were above the levels of recent years, though slaughter was relatively high. Sheep and lamb production in 1936 was less affected by drought than in 1934. The feed position is better for sheep at present than for hogs and cattle, though in the Corn Belt many lamb-feeding areas have short feed supplies.

The 1936 lamb crop was about 9 percent larger than that of 1935 and only slightly smaller than the record lamb crop of 1931. Further expansion in the western sheep industry may be checked, however, by grazing-control measures instituted for the public domain in western areas under the Taylor Act.

The production of shorn wool in 1936 was slightly smaller than in 1935 and total supplies of wool on hand in this country at the end of June were smaller than a year earlier. Wool prices in 1936 rose to the highest levels since 1929. Relatively high wool consumption in Europe and a relatively low foreign wool supply strengthened both foreign and domestic prices.

In the United States, however, the consumption of wool during the first 7 months of 1936 was somewhat below that of the first half of 1935, though above the corresponding monthly average for the last 10 years.

DAIRYING

Increased business activity and fuller employment caused an improvement in the demand for dairy products, while the drought curtailed production. Prices for fluid milk rose and also prices for manufactured dairy products. Butter prices were 100 percent above the low point of the depression. Consumption of fluid milk and cream, which declined in the early years of the depression, turned upward in 1935 and continued upward in 1936. Markets that had been burdened with surpluses faced temporary shortages. The consumption of ice cream, and also of evaporated milk and cheese, increased. With prospects good for further improvement in business activity and employment, the dairy industry expected continued improvement in the demand for its products.

It seems probable that the drought, like that of 1934, will have proportionately less net effect on dairy production than on the output of other livestock products. In 1934–35 total milk production per capita was only about 5 percent below the peak of 1931. Dairy production in 1936–37 will probably be only from 5 to 7 percent less than it would have been had the weather of 1936 been normal. However, the effects of the drought will be felt in 1937–38 in a reduction in the number of cows on farms and in the number of heifers raised. It is expected that the number on farms will decline in 1937 to a relatively low level, owing to the heavy reduction caused by the drought in the supply of feed.

Between January 1, 1927, and January 1, 1934, the number of milk cows on farms increased 21 percent. This was much more than the proportionate increase in the human population. In fact, in 1934 the number of cows per capita was the highest in 35 years. From this point the drought of 1934 caused a decline, which continued in

1935. By January 1, 1936, the number of milk cows per capita was about equal to the average for the 30-year period 1900–1929.

The trade agreement with Canada that went in effect on January 1, 1936, contains provisions affecting the dairy industry. It provides for a reduction of the import duty on cream from 56.6 cents a gallon to 35 cents a gallon on not more than 1,500,000 gallons annually, and also for a reduction in the duty on Cheddar cheese in original loaves from 7 cents a pound, with a minimum of 35 percent ad valorem, to 5 cents a pound, with a minimum of 25 percent ad valorem. However, the reduced rate on cream is 5 cents a gallon higher than the rate established by Presidential proclamation effective June 13, 1929; it is the highest rate on cream the United States has ever had, with the exception of the rate established in the Tariff Act of 1930. The reduction in the rate on Cheddar cheese brings it down to the level that was in effect from September 1922 to June 1930.

In the first 6 months of the agreement the importation of cream amounted to only 6,233 gallons. The total imports of cheese amounted to 24,400,000 pounds—about the same as the relatively low imports of the first half of 1935. Canada contributed about a sixth of the total. In judging the effects of the reduced tariff rate on cheese it should be remembered that less than 6 percent of the milk produced in the United States goes into the production of cheese and also that our imports of Cheddar cheese are a small proportion of our total cheese production. The reductions in the tariff rates on cream and cheese will have little or no effect on the level of dairy prices.

TOBACCO

THE 1936 tobacco crop, on the basis of September 1 indications, was the smallest since 1921 with the exception of the crops of 1932 and 1934. It amounted to 1,142,900,000 pounds, or 11.9 percent below the production of 1935 and 16.2 percent below the average for the 7-year period, 1923–29. Drought conditions were mainly responsible for the reduction. In many tobacco areas the acreage planted exceeded that of 1935. Only the cigar binder, the cigar wrapper, and the Georgia-Florida flue-cured types showed an increase in production. The production of all other types was much below that of last year, and the quality in many of the drought areas was impaired.

However, the stocks of domestic tobacco (farm-sales weight) held by dealers and manufacturers, though 1.5 percent below those of 1935–36, were still 24.6 percent above the 7-year average, 1923–24 to 1929–30. The available supply is estimated at more than 200 million pounds above normal requirements for domestic consumption and exports and for carry-over at the end of the year. The consumption of nearly all tobacco products increased in 1936. In the first 7 months of the year cigarette consumption reached an all-time record for that period. Indications are that the increase will continue. Tobacco consumption per capita does not seem to be much affected by changes in price, but it increases with business recovery and employment. Our tobacco exports increased. Flue-cured tobacco, the predominant export type, represents about 70 percent of the total

exports; and the exports of flue-cured tobacco in the last fiscal year were 32 percent above those of the preceding fiscal year, though 2.3 percent below those of 1933–34. Exports of Maryland tobacco increased in 1936, while exports of other types declined.

Should the weighted average price for all types of tobacco not fall below the August prices for the Georgia and Florida flue-cured type and for the South Carolina flue-cured, the income to farmers from the sale of leaf would be about equal to what it was in 1935.

FRUITS AND VEGETABLES

Fruit and vegetable production, according to the September estimate, was about 11 percent less than in 1935, 9 percent less than in 1934, and about 6 percent below the average for the period 1928–32. Truck crops decreased 13 percent, all fruits 9 percent, potatoes 20 percent, and sweetpotatoes 19 percent. On the other hand, truck crops for fresh market shipment were about 5 percent larger than in 1935. Reduced plantings and the drought were the chief causes of the drop in the production of truck crops for canning, of potatoes, and of sweetpotatoes. Fruit crops suffered comparatively little from the drought, but a severe late spring frost damaged apples, peaches, cherries, and grapes. Favorable growing conditions later failed to offset the damage, though citrus production was larger than in the previous year.

Acreage planted to all truck crops for canning was about 4 percent less than in 1935, but slightly larger than the harvested acreage in 1935 or in any previous year. Abandonment was substantial, owing to the drought. Drought and heat combined reduced the yields, which for all canning crops were about 10 percent below those of the previous year, and, in fact, were the lowest on record. Drought damage was severe to sweet corn, snap beans, and green peas. The total supply of canned vegetables will be about 10 percent below the figure for 1935, but 19 percent above 1934. Production of vegetables for fresh market shipment was higher than in 1935 owing to an increase in the acreage. Yields were generally about the same, though dry weather injured late cabbage. On the whole, the supply of fresh vegetables was ample. Income to the growers, moreover, was higher than for several years.

Potato production was estimated at only 312,000,000 bushels, as compared with 388,000,000 bushels in 1935. The acreage, however, was 10 percent less, and drought damage was severe except in the far West. For the country as a whole the indicated yield was only 97 bushels per acre, as compared with 109.2 bushels in 1935 and a 10-year (1923–32) average of 112.7 bushels. Sweetpotato production, though small in comparison with that of 1935, was above the 5-year (1928–32) average.

In fruit production the 9-percent decline was largely in apples, peaches, cherries, and grapes. The apple crop was 35 percent less than in 1935 and was the smallest since 1921. Production of pears, apricots, fresh plums, prunes, strawberries, cranberries, and citrus was larger than in 1935. Citrus production may be one-sixth larger than last year, while production of all fruits combined, except apples and citrus, may be 12 percent smaller.

POULTRY

WITH poultry flocks not fully recovered from the reductions caused by the 1934 drought, the drought of 1936 is causing reductions again. However, hatchings increased greatly last spring. There will probably be as many laying birds in farm flocks at the beginning of 1937 as there were a year before.

One important effect of the drought will be observed in the relation of egg prices to feed prices. When feed prices rise more than egg prices, sales of laying birds tend to be greater, production per bird declines, and in the spring some reduction in hatching occurs. The hatch of 1935 was reduced following the drought of 1934 because of an unfavorable relationship between feed prices and egg prices. Hatchings in 1937 may decline similarly.

On the whole, prices of eggs and poultry in the first part of 1936 have been favorable to the producer. Poultry prices, however, are now declining. After the drought liquidation ceases they may resume the upward trend of the last 3 years. Egg prices in early 1937, if they follow the course set after the drought of 1934, may continue the present rising tendency.

AGRICULTURAL CREDIT

FARM-CREDIT conditions have improved materially during the last year or so, largely as a result of improvement in farm incomes and a large amount of refinancing for long terms at low rates of interest. In 1935 the demand for farm-mortgage loans declined sharply but remained more nearly steady in the first half of 1936. Private lenders began to return to the farm-loan field; and borrowers had the further advantage of continued low interest rates.

The character of the 1936 mortgage financing, moreover, was very different from that for the last 3 or 4 years. Loan applications to an increasing degree were from farmers who were in no particular emergency. An increasing number of the applications received by Farm Credit Administration agencies were made by young farmers and tenants. The increased prices of farm commodities were encouraging them to try to become farm owners. A large proportion of the other applications were made by farmers interested mainly in refinancing their debts for a long term of years in order to take advantage of the existing low interest rates.

The passing of emergency financing among farmers with a reasonable amount of collateral for farm-mortgage credit is indicated by the decline in the number of applications for loans from the Federal land banks and the Land Bank Commissioner, and by the reentry of private lending agencies into the farm-mortgage field. Applications for land-bank and Commissioner loans declined from 20,000 a week at the peak in 1933 to fewer than 3,000 a week in the summer of 1935 and to an average of 1,620 a week by May 1936. Private lending agencies that were estimated to be doing only about 23 percent of the farm-mortgage business in the first quarter of 1934 and 49 percent during the first quarter of 1935 were doing approximately 70 percent of the business by the middle of 1936.

During the first half of 1936 new loans of the Federal land banks were about offset by repayments and liquidation of loans as their

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loans outstanding remained about steady. Commissioner loans outstanding increased slightly. Loans made by other leading lending agencies did not quite offset repayments and liquidation as their loans outstanding continued to decrease, but at a reduced rate. Furthermore, there was some evidence in farm-mortgage recordings that farm-mortgage loans made by individuals were on the increase. Some debt distress persisted, however, in areas that had suffered partial crop failures for several years, and among farmers whose debt charges reflected previously excessive farm valuations. In spite of this, the general situation had improved to the extent that Commissioner loans, which in amount are about 63 percent second-mortgage loans, were decreasing at a more rapid rate than were the land-bank loans made during the first half of 1936.

The principal backset to a more rapid improvement of the farm-credit situation came when drought developed again this year. As a result, there was an increased demand for loans for relief and rehabilitation by midyear.

Farm-Mortgage Debt

It is unusually difficult just now to estimate the amount of the total farm-mortgage debt in the United States because so much refinancing has been done recently. Adequate statistics are not available to show the net changes produced by the delinquencies, the foreclosures, the compositions, the extensions, and the charge-offs of recent years. The last official estimate placed the amount at $8,000,000,000 as of January 1, 1934. There are no precise data on all the changes that have taken place since then, but indications are that through foreclosures and other means the total has been brought down somewhat from the 1934 figure. Needless to say, the amount of the farm debt does not by itself indicate the financial position of the farmers. Whether or not it is burdensome depends on the size of the debt relative to the farm income out of which principal and interest payments can be made.

Licensed member banks of the Federal Reserve System held farm-mortgage loans amounting to $253,000,000 in the first quarter of 1936, as compared with $263,000,000 in the first quarter of 1935. Farm-mortgage loans held by agencies of the Farm Credit Administration totaled $2,869,089,100 in January 1936, as compared with $2,586,206,691 in January 1935. These figures, however, do not indicate the whole trend, as financing through other agencies is quite important, though details are not available.

Farm borrowing for current production increased during the past year. Agricultural prices were at the highest level since 1930, and some expansion took place in farm acreage and livestock breeding. Many country banks increased their loans to farmers for current production, though frequently their total loans showed little change. Lending by the production-credit associations of the Farm Credit Administration increased. In May 1936 the outstanding loans of these production-credit associations totaled $135,467,214, as compared with $101,269,485 in May 1935. It is characteristic of the early phases of agricultural revival for current production loans to increase more rapidly than mortgage financing.

Federal credit agencies during the year aided farmers through low interest rates. Interest rates on outstanding Federal land-bank loans, which had been temporarily reduced in 1935 to 3½ percent, were continued by legislation on that basis for the period ending June 30, 1937. On new mortgage loans the Federal land banks continued to charge 4 percent per annum. Other financing agencies offered low interest rates likewise, and the first half of 1936 saw some increase in farm-mortgage lending. Feed and seed loans made by the Federal Government, new lending by commercial banks, and loans from the production-credit associations helped farmers in some areas to pay cash for more of their supplies and reduced the volume of costly store credit. The Resettlement Administration enlarged its activities in handling distress cases; and by April 1936 its total loan commitments had risen to $53,793,000. After the drought the volume increased more rapidly.

The drought, of course, is complicating the farm-credit situation and delaying liquidation. Short-term credit by the Farm Credit Administration agencies and by commercial banks amounted at the end of 1934 to about $1,121,000,000. Other personal loans, store credit, credit extended by implement firms, and loans negotiated by farmers' cooperative associations made up an important additional amount. Probably the total short-term credit outstanding did not change greatly between the end of 1934 and the middle of 1936, as country-bank loans outstanding continued to decline and outstanding short-term loans by Farm Credit Administration agencies continued a steady increase.

Character of New Short-Term Credit

As in the case of farm-mortgage credit, more important than any change in the amount of short-term credit outstanding was the change in the character of the new short-term credit being extended during the first half of 1936. More of it was for productive purposes and less of it for emergency financing of old debts. As an example, total short-term credit extended by Farm Credit Administration agencies, including the emergency and relief agencies during the first half of 1936 declined steadily and was less than for the same period the year before. On the other hand, loans made by the production-credit associations alone increased during the first half of 1936 and were larger than for the same period a year earlier.

After the midyear, however, the drought increased the demand for short-term credit of a relief nature, which had fallen off in the spring months of 1936. Emergency crop loans and drought-relief loans outstanding have steadily increased since 1929 and 1930 and now constitute more than 40 percent of the total outstanding short-term credit administered by the Farm Credit Administration. In addition, loans or grants in the more distressed cases are being made by the Resettlement Administration.

AGRICULTURAL TAXES

Tax levies per acre on farm real estate have changed on an average very little in the last 3 years. They run about 54 percent above prewar (1913) level and about 36 percent below the level of the peak year 1929. Factors governing the farm-taxation trend include, of

course, the volume of the farm income, the expenses of local and State government, and the extent to which taxing bodies rely on the property tax for revenue. With respect to all these factors there are some favorable indications.

As indicated earlier in this report, the outlook for the national farm income is favorable despite this year's drought, though the regional distribution will be extremely abnormal. There is a possibility of continued economies in local and State expenses. Further drastic cuts, however, are unlikely as great curtailment has already been accomplished; moreover, local bodies may have to assume more responsibility for activities recently supported heavily by Federal aid. As to the place of the property tax in State and local revenues, progress is being made toward developing additional sources, and toward shifting part of the burden from real estate to other forms of taxpaying ability.

Some of the reductions that have been made in farm-realty taxation are the result of curtailment in essential public services. For example, school terms have been reduced and teachers' salaries lowered. School budgets, in fact, have been drastically cut in many areas. Relief and rehabilitation expenditures have been extremely heavy, but the diversion of these expenditures to State sales and to Federal taxation has been a factor in lowering the farm-tax burden. As yet not much farm-tax relief has come from the reorganization of local and State governmental machinery, though this method offers important opportunities.

Improvement in farm income will have a dual effect on the farm-tax situation. It will decrease the burdensomeness of any given tax payment, but it will also lessen the economic pressure toward further tax decrease and even toward continuation at the present level. As mentioned above, many of the decreases in real estate taxes during the past several years have been made possible by curtailment of basic governmental services. Such curtailments have in many communities been deplored and have been considered only temporary expedients. With further improvement in the economic situation and in farm income there undoubtedly will be a decided tendency to restore the curtailed services to their previous levels. The tendency probably will extend also to increases in any services which before the recent curtailment had been locally considered as inadequate.

Over a long period of years preceding 1929 there had been a practically continuous increase in average farm real-estate taxes per acre for the country as a whole. This is demonstrated by a preliminary index computed by the Bureau of Agricultural Economics for the period 1890 to 1913, coupled with the Bureau's current series (1913–34) and a preliminary 1935 estimate. These series indicate an increase of about 267 percent in farm real-estate taxes per acre from 1890 to 1935. General price levels for the period increased about 40 percent, but even if adjustment is made for the price factor, there remains an increase of over 160 percent in farm real-estate taxes per acre. This figure of 160 percent should not be assumed to be altogether accurate, because changes in the general price level may not well represent changes in the composite price of governmental services, but it is believed to be a useful approximation for

the present purpose. On the assumption that local-government efficiency remained the same, these increases beyond the increase in prices should largely represent increase in governmental services.

The importance of this trend as it affects the future is its suggestion of a more or less constant demand for expansion of the services furnished by local and State governments. So long as such demand continues, there probably will be a decided tendency for farm taxes to increase in periods when farm income is relatively satisfactory and taxes are consequently less burdensome. The effect of this again will be influenced by any substitution of other tax sources for real-estate taxes.

There is heavy accumulated delinquency in farm taxation in many States. The acreage delinquent seems to have reached a maximum in 1932. Probably the amount of taxes delinquent continued to increase until 1934. These arrears, which farmers are beginning to pay up, often exceed their current tax bills, and farmers' tax payments in many cases will similarly exceed their bills for current taxes.

MARKETING AGREEMENTS

Marketing programs authorized in the original Agricultural Adjustment Act and modified under the subsequent amendments continue to help farmers to sell milk, fruits, and vegetables to better advantage. As of July 1, 1936, there were in effect 39 marketing-agreement, order, or license programs. They included 21 licenses and 3 orders for fluid-milk markets, 1 marketing agreement and 1 license for the national evaporated-milk industry, 1 marketing agreement for the national dry skim-milk industry, and 11 marketing agreements supplemented by 4 licenses and 6 orders for 11 such crops as fruits, nuts, and vegetables. With processors, handlers, and farmers' cooperative associations acting together under these programs, destructive competition has diminished, and more stable marketing conditions have been established. Launched as emergency measures, the programs have come to be valued for permanent use. Many of the more successful have been built on foundations already laid by the farmers' cooperatives. Others have given the initial impulse to cooperative marketing in various localities. They have helped farmers to coordinate marketing with production and to apply up-to-date methods of sorting, grading, and distribution.

After the decision of the United States Supreme Court in the *Hoosac Mills case*, it became necessary to reorganize the administrative set-up for dealing with marketing programs. Marketing activities that had previously been handled by the commodity divisions of the A. A. A. were centered in the Division of Marketing and Marketing Agreements. Meantime, regional divisions were established for administering the Soil Conservation and Domestic Allotment Act. The A. A. A. continued to develop and administer marketing programs, because the sections of the act relating to these activities were not before the court in the *Hoosac Mills case.* In subsequent suits, however, the marketing-agreement provisions of the Agricultural Adjustment Act have been questioned. The issue is whether the Hoosac Mills decision did or did not invalidate the marketing-agreement features along with the crop-control provisions of the act.

Final determination of the matter awaits action by the Supreme Court. In two out of three cases considered by Federal district courts, the marketing-program provisions of the Agricultural Adjustment Act have been upheld. In *United States* v. *Hugh David Edwards*, Judge Yankwich, of the United States District Court for the Southern District of California, found the marketing-agreement and order sections of the act to be separable from the crop-adjustment and processing-tax provisions. In *United States* v. *David Buttrick et al.*, Judge Brewster, of the United States District Court of Massachusetts, took a contrary view. He held that the marketing-agreement and order provisions were inseparable from the crop-control and processing-tax provisions. Later, in *United States* v. *Jerry Buckley et al.*, Judge St. Sure, in the United States District Court for the Northern District of California, continued in effect a restraining order that had been issued to halt violations of an order issued by the Secretary regulating the handling of deciduous-tree fruits.

As required by the amendments to the Agricultural Adjustment Act which were approved August 27, 1935, the Administration is replacing licenses with orders and carrying out the other requirements of the amended act. It has been possible to establish for various milk areas conditions tending to give all the producers an equitable share in the market. The agreements and orders usually provide for the classification of milk according to its use by the handlers; for the payment of minimum prices by handlers, and for the payment of uniform returns to producers under pool plans. Programs for the marketing of fruits and vegetables are simpler. They deal principally with the rate at which produce is shipped to market and tend to adjust market supplies more nearly to the prevailing demand. They affect, of course, only commodities already produced and ready for market. Additional programs are being developed at the request of producers and handlers, with the latter group showing an increased recognition of the fact that they have a common interest with farmers in the maintenance of fair prices to producers.

Surplus-Removal Operations

Surplus-removal operations have been developed as a supplement to the marketing-agreement programs. The authority is section 32 of the amendments of August 1935 to the Agricultural Adjustment Act. This section makes available an amount equal to 30 percent of the annual customs receipts for the encouragement of exports and the diversion of surpluses to other uses. Congress has subsequently amended it so as to include Government purchases of surplus farm products for relief distribution. The funds it makes available are in addition to congressional appropriations for the purchase of surplus dairy products for relief distribution. Operations under the section have dealt effectively with a number of farm-surplus situations, though the method is not universally applicable.

Advantages have resulted both to producers and to the needy. Surpluses that might otherwise have gone to waste have been moved into consumption, with a net gain both in farmers' prices and in food consumption among low-income groups. The purchases for relief

distribution have included apples, citrus fruits, prunes, pears, dried beans and peas, onions, turnips, cabbage, carrots, and eggs. In addition, the funds available under section 32 have made it possible to find new uses and new outlets for some farm products. More than a dozen surplus-diversion programs are in operation, under agreements between the Secretary and organizations of producers and handlers. They include programs for walnuts, pecans, raisins, prunes, dried figs, California fall and winter pears, dark air-cured and fire-cured tobacco, peanuts, and cotton.

The diversion programs authorize purchase of the commodities on the basis of grades or other requirements, at prices approved by the Secretary of Agriculture. The industry groups sell the products to anyone who will contract to convert them into byproduct or other authorized uses. Differences between the prices received and the prices paid for the products, plus incidental handling costs, are made up out of section 32 funds. Other types of diversion programs do not involve agreements between the Secretary and any industrial group. In these cases the diversion payment goes directly to individuals who comply with the requirements. For example, in a program designed to increase the exportation of pecans, the diversion payment went to the exporters and represented the difference between the domestic buying price and the export selling price.

The benefits have much exceeded the costs. Purchases of prunes for relief distribution involved only a small outlay; but the operation prevented a disastrous break in prune prices, and in fact caused an advance in the market for the entire crop. Frequently the diversion of surpluses into relief or other channels outside the usual course of trade brought about an increased distribution of the commodities through ordinary trade channels. It had this effect because the resulting price gain removed any incentive to let the products go to waste. Certain of the diversion programs include efforts to develop and expand uses for various products. In other cases, as for example, the export program for pecans, the programs introduced the commodity into markets previously unfamiliar with it.

Marketing Problems

The farmer's interest in marketing is less direct than his interest in production, because as an individual he must take the marketing system about as he finds it. It requires group action, such as the organization of cooperative associations or the passage of legislation, to make significant changes in the marketing system. There are some things the individual farmer can do. He may choose between grading his crop, or selling it field run; between selling it at harvest time or storing it; and between selling it to a local buyer or to dealers in central or terminal markets. Sometimes he can sell direct to the consumers. Federal inspection services, and the Federal market-news service, give the farmer increased facility in marketing. But as an individual there is not much he can do to lower the costs of marketing or to make the distribution system operate more smoothly.

Farmers believe, however, that substantial improvements can be effected through legislation and through cooperative action. They are impressed with the size of the national bill for transportation,

processing, and marketing. Even before the depression, in the decade of the 1920's, transportation, processing, and marketing absorbed about 55 cents of the consumer's food dollar. At the bottom of the depression these services absorbed about 67 cents. Since 1933 the proportion left to the farmer has increased, but it is not yet back to what it was before 1929. This fact is not in itself a proof that marketing and distribution are inefficient or extortionate; but it is evident that we need to be concerned with the cost of these services fully as much as with the costs of production on the farm. The whole subject needs thorough study; and farmers' organizations show an increasing awareness of the fact.

One way to reduce the costs of marketing and distribution is to suppress unfair and dishonest trade practices and to prevent racketeering. Enforcement of the Perishable Agricultural Commodities Act, the Packers and Stockyards Act, the Grain Futures Act, and the Food and Drug Administration Act has had a salutary influence. Investigations by the Federal Trade Commission have raised the standards of commercial practice. Trade regulation by State and municipal authorities contributes to the same end; in fact, many phases of agricultural marketing are necessarily in State and local jurisdiction, since they do not affect interstate commerce directly. But the problem usually transcends local or State lines. It is obvious, for example, that the California artichoke grower has a direct interest in preventing an artichoke racket in eastern markets. In many cases Federal, State, and local authorities must cooperate in preventing unfair trade practices, and perhaps in working out coordinated programs for improvement.

Research and service agencies, both Federal and State, must go beyond the provision of commodity inspection and market news, and the suppression of unfair trade practices. There is need for a positive program to improve the marketing system. Much could be done to promote efficient, low-cost handling of commodities, and to improve both the placing and the timing of the distribution. Many crops do not yet go to all the places where they could be profitably sold, and do not reach all their possible markets at the most advantageous moment. There is a field here for significant improvement. But the problem is so intricate and involves so many aspects of intercommodity competition that cooperative study seems indispensable to effective Federal and State action.

Rapid Progress Unlikely

It is unwise to expect extremely rapid progress. Our delicate and complicated marketing system has evolved gradually, in response to gradually changing conditions. Sudden and drastic overhauling might wreck it. But adjustments here and there are urgently needed. Recent years have seen important developments to which parts of the marketing system have not become well-adapted. The growth of large-scale processing and distribution raises new marketing problems. Motortruck transportation, commodity exchanges, and direct buying also have an important bearing on the marketing process. Study of these matters is a necessary preliminary to the development

of a legislative policy that will be fair to producers, distributors, and consumers.

One part of the marketing machinery which obviously needs adjustment is the wholesale and jobbing markets for perishables. In many large cities the cost of marketing and distributing perishables seems unnecessarily high. City marketing facilities have not been fully adapted to the motortruck, to direct purchasing by chain stores, and to other recent developments. Competitive building of railway-terminal facilities has tended to split markets and has added to the costs of both buyer and seller. Trucking and rehandling could be greatly reduced in many large cities through better coordination of the available facilities. A related problem arises from the development of regional or concentration points in the country. Several types of regional markets have grown rapidly since the beginning of the depression, and continuation of the growth will require research to keep it on sound lines.

An alarming development is a tendency toward the exclusion of outside foods from some markets and some States. Local protectionism of this type is profoundly repugnant to the spirit of our institutions and diminishes the Nation's prosperity exactly in the same manner as the excessive development of international tariffs diminishes the volume of international trade. Among the causes of this country's prosperity in the past, free trade among the States ranks high; and no consideration of a purely local nature should be allowed to interfere with it.

In the handling of certain products, for example milk, health factors enter; and the right of the several States to impose and enforce sanitary regulations cannot be questioned. In other cases it may be necessary to limit free trade in order to prevent the spread of insect pests or diseases, or for other sound reasons of public policy. No one should object to such legislation when it really contributes to national welfare. But there can be little doubt that in some cases the welfare of consumers and similar considerations have been used as an argument for regulations the main purpose of which is to benefit one group of producers at the expense of other groups.

Such legislation, if it is effective at all, prevents efficient production and efficient marketing. If carried to extremes it will raise food prices and lower consumption without benefiting producers. Temporary advantages gained by producers in one locality may be nullified by retaliatory legislation in other localities. It is extremely important to maintain among the States as high a degree of free trade as is consistent with the other legitimate objects of public policy.

INSECT CONDITIONS

Climatic factors played an important part during the year in the abundance and destructiveness of many major insect pests. The tent caterpillar and canker worms continued to occur in outbreak numbers in many sections of the Eastern States, and to defoliate trees over rather large areas. In the same general region, however, the codling moth and the oriental fruit moth were less abundant than normally. One of the introduced sawflies which feeds on grasses and grains was unusually abundant and destroyed wheat plants in

certain parts of the upper Ohio Valley. Various kinds of cutworms were destructively abundant generally throughout the region east of the one hundredth meridian. The cotton boll weevil was less destructive than in average years. The cotton leafworm invaded the fields unusually early, stripping the plants over large areas in Texas and adjoining States in the Cotton Belt. The bollworm, or corn earworm, was more destructive to cotton than in any year since 1929, but was generally scarce in corn over the eastern half of the country. It occurred in outbreak numbers in many sections in the west, and caused material losses of tomatoes. The house cricket was unusually abundant in many localities in the East. The abundance of these and many other insects is affected rather directly by the weather conditions. Some kinds, for example the periodical cicada, which occurred this last spring generally throughout the United States, are little affected by changes in weather conditions.

A few of the less familiar insect pests, such as the vetch weevil, the pepper weevil, tomato pinworm, cherry scale, and vegetable weevil, were found in new localities. A scale insect which had not previously been reported from the United States was discovered in a limited area in California and eradicated by the cooperative effort of State and Federal agencies.

During the summer of 1935 grasshoppers occurred in outbreak numbers in several of the Western and Middle Western States, but not to the same extent as they did in 1934. During the 1935 season the application of poison bait left over from the previous year materially contributed to reducing their numbers and protecting crops in several of the more severely infested States of the northern Plains region, particularly North Dakota. Drought conditions in the spring of 1936 were, however, very favorable for the development of grasshoppers, and outbreaks, accompanied by material damage, occurred in Nebraska, Iowa, Kansas, Missouri, Oklahoma, Minnesota, Montana, New Mexico, Arkansas, and eastern Colorado. This condition was anticipated and State officials for those sections, where cooperative surveys had been made the previous fall, were fully informed as to the possibility of grasshopper outbreaks, together with the estimate of the amount of material that would be needed to combat them. The area surveyed did not include Missouri, Oklahoma, and Arkansas, and accurate information was not available as to the sections of these States where the outbreaks were expected.

Limited amounts of bait materials left over from the previous control campaigns or secured through local and State agencies were available in a few sections only. These amounts, together with those secured with the special congressional appropriation of $250,000, made late in June 1936, were not adequate to meet the need, and farmers were urged to secure and distribute additional bait to protect their crops and reduce the numbers which menace next year's crops. The grasshoppers developed into winged forms perhaps a month earlier than usual and in the absence of food and effective control moved generally throughout the area, including sections where they had not been abundant previously.

The great numbers of chinch bugs that entered hibernation in the fall of 1934 presaged the most-severe outbreak of this pest in 50

years. Fortunately, the cold, wet spring which occurred over most of the area was so destructive to the bugs that outbreaks developed only in a few sections. It was, therefore, not necessary to use the special authorization and appropriation for chinch-bug control in the summer of 1935, and only $48,000 was expended of the $2,000,000 provided as an insurance fund to protect corn from bugs of the first generation.

The European corn borer caused severe damage in limited areas along the eastern seaboard, particularly to sweet corn. With the aid of an allotment from emergency funds, a survey was carried on to determine its spread, distribution, and relative abundance throughout the previously known infested area. To determine the status in the known infested area, 1,124 townships and 64 counties of 11 States were surveyed. During this survey 5,817 fields and 32,578 acres of corn were inspected. This survey disclosed that there was a general increase in borer abundance through much of the infested area. To determine the possible spread of the borer into new areas, scouts visited 712 townships in 28 counties in 11 States, examining 14,690 fields, totaling 192,222 acres. New infestations were found in 237 townships, but all of these were adjacent to areas previously known to be infested. This indicates that the spread had occurred largely by natural means.

The infestation of screwworm, first discovered in the Southeastern States in the fall of 1933, continued but was very materially reduced, largely because of the adoption of methods of treatment and handling livestock recommended during the cooperative educational campaign in 1935. The special appropriation of $480,000 which provided for the cooperative educational campaign made it possible to acquaint stockmen and others throughout the newly infested area with the approved methods of combating screwworms. During the summer of 1935 screwworms were unusually abundant throughout the Southwest, where infestation has annually caused material losses to cattle, sheep, and goats.

The educational and demonstrational work on screwworm control was extended to this section in the spring of 1936, and is now being conducted throughout the area infested by this pest. The extension and continuation of the work is provided for by an additional special appropriation of $460,000. The low temperatures which occurred during the winter over much of this area, together with the effective effort of combating the screwworm in areas where it overwintered, urged as a part of the educational campaign, greatly reduced the number of screwworm cases throughout the infested area. While the research to improve control measures should continue, the cooperative educational work can be brought to a close during the current year.

Plant-Pest Control

The date palm scale, an important introduced insect which at one time appeared to be the limiting factor to the development of date culture in the Southwestern States, has been eradicated from the United States. Continued intensive inspections failed to disclose the presence of this pest, and eradication activities begun a number of years ago were discontinued at the end of the fiscal year. At the same

time the quarantine regulating the movement of date palms in the United States was withdrawn.

The restrictions governing the importation of plants likely to introduce this and other pests continue in effect. These and other regulations were studied, however, to determine whether conditions had altered sufficiently to justify modification of the requirements. Two special quarantines restricting the entry of pines were in fact rescinded, the evidence indicating that adequate protection was included under another quarantine.

Regular activities carried on in cooperation with State agencies for the control of plant pests were augmented by allotments from emergency funds to provide relief employment. Trained workers planned, organized, and directed the expansion of these activities so as to use relief labor effectively. At the peak of the active season 25,242 workers were employed in 1,497 counties in 44 States, and during the year the work provided 21,398,000 man-hours of employment. The regular activities expanded and benefited by this employment are: White-pine blister-rust control; gypsy-moth control; phony-peach eradication; citrus-canker eradication; barberry eradication; and the eradication of the Dutch elm disease. In some instances, including the gypsy-moth campaign east of the barrier zone, barberry eradication in Pennsylvania, West Virginia, and Virginia, and white-pine blister-rust eradication in the Appalachian Mountain States, the work was extended into sections not previously covered with regular funds.

The brown-tail moth, an introduced pest which has been present for many years in part of the New England States, though its spread into other sections has been prevented by the enforcement of a Federal quarantine, was combated in the infested area by relief workers employed under a special allotment. They destroyed millions of the webs in which the pest overwinters. The work of destroying wild cotton in southern Florida to eliminate the pink bollworm and protect the Cotton Belt against this pest, was expanded by relief employment. To lessen the risk of the spread of the dry-land form of the cotton boll weevil, of which wild cotton is a native host, relief labor employed under a special allotment located and destroyed 615,596 *Thurberia* plants in 163 square miles in the Tortollita Mountains of southeastern Arizona.

With the aid of emergency funds, the eradication of peach mosaic, a disease of major importance to peach culture recently discovered in certain western areas, was undertaken in cooperation with State agencies. This infectious disease materially affects the growth of the peach tree and causes the production of small knobby fruit of little commercial value. It was first discovered in Texas. A few infected trees were reported from western Colorado in 1934, and in the spring of 1935 thousands of infected trees were located in three western counties of this State. The only known way of combating the disease is to locate and destroy infected trees. Through the cooperative eradication effort thousands of infected trees were destroyed in western Colorado during the summer of 1935. Surveys so far conducted in 1936 disclose the presence of only a comparatively few infected trees in this area and demonstrate the effectiveness of the eradication work. Within the last few months the disease has

also been located in parts of California, Utah, and New Mexico. Plans to extend the eradication effort to these sections are being perfected. Outlying infections may have been established through the movement of infected nursery stock.

The Dutch elm disease, which threatens the destruction of elms throughout the country, is an important problem in plant-pest control. Only a small amount of regular funds was provided to combat this disease. Allotments have been made from emergency funds and the cooperative eradication work pushed. The personnel-selection requirement, the necessity for training scouts and workers, and the uncertainty as to when and in what amount funds would be available, increased the difficulties. A few infected trees were found at outlying points, notably at Brunswick, Md., and Norfolk and Portsmouth, Va.; Old Lyme, Conn.; and Indianapolis, Ind. The infected trees were promptly destroyed. In the more heavily infected area—within a 50-mile radius of New York Harbor—the work included not only the location and removal of trees known to be infected, but also the location and removal of sick and dying trees, which may not only harbor the disease but may also serve as breeding places for the insect known to transmit the disease. All but a few of the 14,000 or so infected trees so far discovered in the United States were destroyed at the close of the fiscal year. Scouting during the past spring and early summer—the season most favorable for the location of infected trees—disclosed the presence of only a few infected trees as compared with the numbers discovered during the comparable period in 1935. This appears to demonstrate the practicability of eradicating the disease by methods used, the only ones known to be effective.

Research on Insects

Research to determine effective ways of combating insect pests has continued along many lines. In the search for new insecticides, especially ones which will not leave harmful residues on the marketed food product, the chemists have synthesized more than 100 organic compounds which have been tested by the entomologists to determine their effect on insects. In the initial tests some 20 of these, mostly those in the azo group, were very toxic to insects and appeared to hold promise for use in combating at least certain kinds of insect pests.

Detailed studies of pyrethrum demonstrated that the chemical formula for the toxic principles from pyrethrum flowers is much simpler than had been believed. This discovery may make it possible to develop the active principles of these flowers synthetically. At present our only source for this valuable insecticide is the imported flowers, approximating 10 million pounds annually. New compounds of nicotine have been made. Two promising ones are prepared from nicotine and peat, one soluble and the other insoluble in water. These are being tested on various insects including the codling moth, the principal pest of apples. An improved method of analyzing small amounts of nicotine opens up new ways of using this material, particularly as a fumigant. It has been demonstrated that the nicotine present in certain common types of tobacco is not present as a glucoside. This discovery has a practical bearing on the

preparation of home-made tobacco preparations used for control of various insects.

Laboratory and field tests with organic insecticides, particularly derris and cubé, have brought many modifications in the recommendations for the control of certain insect pests. It has been demonstrated that these insecticides which do not leave residues objectionable from the standpoint of human health can be effectively used against a number of different truck-crop pests, such as certain cabbage worms and the Mexican bean beetle, and that they are effective against flea beetles destructive to growing tobacco. The further usefulness of these recently developed materials is evidenced by the determination that one application of sprays or dusts of derris or cubé is effective against the pea aphid over a longer period than other recommended materials such as pyrethrum and nicotine. The practicability of protecting sugar beets grown for seed purposes from destruction by curly top by the application of pyrethrum and oil as an atomized mist has also been demonstrated.

The low per-acre value of most cereal and forage crops prevents the use of direct measures to control certain important insect pests, and cultural and biological control methods are not always effective, particularly because community action is usually required. Various varieties and strains of these crops have shown marked insect resistance, and investigations along this line have been intensified. Certain strains of field corn have been demonstrated to have marked resistance to the European corn borer independent of the time of maturity of the corn. One of the important factors in cutting down infestation is a delayed tasseling common to certain inbreds. No resistant character has, however, so far been found in sweet-corn varieties and strains which is not directly associated with date of maturity. Strains of alfalfa entirely immune to alfalfa-aphid attack have been obtained by selection. Marked progress has been made in developing wheats suitable for California, Kansas, and Indiana conditions which are resistant to the hessian fly. A variety of wheat substantially immune to fly attack has been developed in California, and the incorporation of this characteristic in varieties suitable for commercial use is under way in cooperation with plant breeders.

Two varieties of soft red winter wheat highly resistant to fly attack have been discovered in Indiana. Certain varieties of hard red winter wheat have been discovered which may be utilized in producing suitable wheats for production in Kansas and surrounding States. Studies on chinch bug in sorghum and wheat have revealed that certain varieties of both of these crops show marked resistance to chinch-bug attack. The development and use of these may offer a means of avoiding the heavy annual losses, including those occurring during chinch-bug outbreaks, such as that of 1934. Certain varieties of field and sweet corn are definitely less susceptible than others to attack by the corn earworm. The practical possibilities of this discovery have not, however, been determined.

Investigations to determine the possibility of using predacious and parasitic insects as aids in combating injurious insect pests have been extended to new fields and include such pests as the pea moth, the lima-bean-pod borer, and the pea weevil. An allotment from the

sugar-processing-tax funds from Hawaii provided for expeditions to Africa, South America, and the Orient in search of natural enemies to aid in combating the Mediterranean fruitfly and the melonfly in Hawaii. The introduction of natural enemies of insect pests into Puerto Rico, including an expedition to South America, was supported from a similar allotment from Puerto Rican tax funds. Eight beneficial insects have already been recovered on that island, three of which are well established and are being recolonized in parts of the mainland. Cooperative observations in Cuba fully substantiated the previous reports that the parasite of the citrus blackfly introduced on that island in cooperation with the Cuban Government in 1930 is effective in controlling this pest and reducing the possibility of its reaching our shores.

Studies on the secretions from the larvae of those species of flies used in treating chronic ulcers and bone lesions disclosed that one of the secretions is urea, a well-known chemical, which is widely used and produced synthetically. Reports received from physicians and surgeons who cooperated in testing urea produced synthetically, and chemically identical with that in the fly secretion, suggest that it contributes to the healing of certain types of wounds and has a soothing and beneficial action on many kinds of skin infections as well as deep-seated wounds. This discovery, if supported by further investigations, may be of material benefit to the medical profession and may reduce human suffering.

CHEMISTRY AND SOILS RESEARCH

Chemists in the Bureau of Chemistry and Soils have long been engaged in developing useful products from agricultural raw materials such as straw, cobs, fruit, and vegetable culls, and other byproducts of agriculture. Farm byproducts constitute more than 60 percent of the material annually removed from the land. These materials are part of the farmer's assets, as they are the fruits of his labor and of the fertility of the land. The straw, stalks, hulls, and other residues of the leading crops amount annually to more than 260,000,000 tons and contain approximately 115,000,000 tons of cellulose, 66,000,000 tons of pentosans, and 53,000,000 tons of lignin. A large proportion of this material, now wasted, is available for industrial utilization.

Efforts by Department chemists to tap this reserve of potential wealth have yielded substantial results, among the more recent of which may be mentioned a process for making high-grade cellulose from sugarcane bagasse, methods for producing furfural cheaply from cobs or hulls, a continuous destructive-distillation process for making charcoal and useful chemicals from various crop wastes, and fermentation processes for the production of fuel gas, organic acids, solvents, and residual cellulose fibers from crop wastes.

For the utilization of surplus agricultural products and culls the chemists of the Department have developed processes for making commercial products from citrus fruits, a process for the extraction of starch for industrial uses from sweetpotatoes, and mold-fermentation processes for making organic acids from corn sugar. Improved methods of using cornstalks and cereal straws for making

high-grade papers have received much attention, though the competition of other raw materials impedes commercial progress.

Chemical research in the Department during the last year contributed materially to the growing fund of knowledge of the utilization of agricultural products and byproducts. In cooperation with the Texas Agricultural Experiment Station, and using laboratories furnished by local chambers of commerce, the Department's chemists further studied the utilization of surplus citrus fruits, culls, and byproducts. They gave special attention to the production of fruit juices and concentrates, alcoholic beverages, vinegar, marmalade, candy, and volatile oil. Several commercial firms cooperated. That this work is valuable is attested by the fact that the number of commercial plants utilizing citrus culls in Texas increased from 3 in 1933 to 17 in 1935. In the same period the amount of money paid annually to growers in that State for citrus culls increased from $10,000 to $250,000.

In California investigators studied the production of wines and brandies from surplus and cull deciduous fruits, the loosening of stick-tight walnut hulls by ethylene, the preservation of fruit and fruit pulps by freezing, and the production of sirups and concentrates from apples, pears, and dates. In cooperation with the Washington State College of Agriculture and Agricultural Experiment Station, the Department established a new laboratory at Pullman, Wash., known as the Fruit and Vegetable Byproducts Laboratory, where it will investigate the utilization of fruits and vegetables grown in that section.

Experimentation at Byproducts Laboratory

Work proceeded at the agricultural byproducts laboratory at Ames, Iowa, on the production of cellulose, paper pulp, destructive-distillation products, and fermentation products from crop wastes. In these studies the Department cooperates with Iowa State College. In cooperation with the New York Agricultural Experiment Station at Geneva, N. Y., the Department is investigating the utilization of grapes, berries, and other fruits in the manufacture of commercial fruit juices, wines, and beverages. In cooperation with Stanford University the Department is studying at San Francisco the pharmacology of insecticidal materials. In Louisiana with the assistance of the Louisiana Agricultural Experiment Station, the Department is investigating the influence of cultural conditions on the composition and workability of juices from different varieties of sugarcane and the prevention of deterioration in harvested sugarcane during short-time storage. In cooperation with the North Carolina Agricultural Experiment Station the commercial fermentation of cucumbers into pickles and related products under southern climatic conditions is being studied.

Commercial development of a process discovered in the Department for producing sweetpotato starch is going forward under the leadership of the Bureau of Chemistry and Soils, in cooperation with the Bureau of Plant Industry and the Mississippi Agricultural Experiment Station, at a plant operated by a farmers' cooperative association at Laurel, Miss. In cooperation with the Alabama Poly-

technic Institute the Bureau of Chemistry and Soils established a field laboratory at Auburn, Ala., to promote the industrial utilization of sweetpotato starch. The Chemical Foundation recently established a research fellowship in the Bureau to find new technical uses for sweetpotato starch. Studies are in progress in cooperation with the Mississippi Agricultural Experiment Station on the quality and composition of sirups prepared from different portions of sorgo stalks. Improved methods developed by the Department for making sorgo sirup and sugarcane sirup are being introduced in Mississippi. Alabama, and Florida. The Texas Agricultural Experiment Station recently demonstrated the use of farm-scale equipment in making high-grade sugarcane sirup by the Department's method.

Cooperation was extended from the Department to a commercial firm in developing the improved nitric-acid process for producing cellulose from bagasse. Cooperation with commercial firms advanced also the technique of utilizing byproduct milk sugar in fondants for confectionery, and in determining the yield and quality of paper pulp from wheat straw, flax straw, cornstalks, and artichoke tops. In the last-mentioned experiments the Department's investigators used patented equipment designed for the production of paper pulp from straw by a continuous soda cooking process at atmospheric pressure.

Fundamental Research on Proteins and Enzymes

Fundamental research in the Bureau of Chemistry and Soils dealt with the chemistry of proteins, enzymes, plant pigments, cuticle waxes of fruits, lignin, turpentine, resin acids, and vegetable oils; also with the chemistry and physics of soils, the chemistry and physics of elements and compounds in fertilizer materials, the pharmacology of insecticides that may contaminate fruits and vegetables, and with microbiology as it relates to food spoilage, food preparation and preservation, industrial fermentations, and the curing of hides and skins. As part of a basic-research program provided for in the Bankhead-Jones Act of June 29, 1935, the Bureau organized three new research projects. These are: (1) Research into the industrial utilization of the soybean and soybean products, (2) the chemistry of enzymes and of enzyme action at low temperatures, and (3) a study of the allergens of agricultural products. In addition, chemists and plant pathologists will cooperate in a Bankhead-Jones project for the study of plant viruses.

The work on soybeans and soybean products is going forward at the Regional Soybean Industrial Products Laboratory, which has been established at the University of Illinois, in cooperation with the agricultural experiment stations of the 12 Corn Belt States. Specialists from the agricultural experiment stations will cooperate with chemists and agronomists from this Department. The object is to improve the quality and increase the yield of soybean products, and especially to develop industrial uses for them. It will include the selection of types and varieties for particular purposes. In the fundamental studies of enzyme action several of this Department's bureaus will cooperate. Special interest attaches to the little-understood activity of enzymes at low temperatures because such activity

affects frozen and cold-storage products in many ways. The work on allergens should yield information about the chemical nature of the plant and animal products known to cause physical ailments such as rash, hives, hay fever, and asthma, in susceptible persons. It has been estimated that 10 percent of the population is allergic.

Anticipating the eventual need for motor fuels other than gasoline, the Bureau of Chemistry and Soils is expanding its investigations into the possibility of producing such fuels economically from farm products and byproducts. One line of research will explore the efficiency of the microbiological conversion of starch and sugars into alcohol or other liquid compounds having fuel value. In the production of industrial alcohol in the past, it has always been necessary to give due consideration to the possibility that the alcohol might be used in such a way that its potability would be of primary importance. However, in the production of power alcohol from farm products potability is not a factor. It is possible, therefore, that fermentative processes based on this conception of the function of the end product may yield greater amounts of liquid fuel at a lower production cost. It is planned to give careful attention to this phase of the liquid-fuel problem. The possibility of using solid fuels, derived from agricultural products, in internal-combustion engines will also receive attention.

The Soil Survey

Another branch of the Bureau's work is the soil survey. Fundamental knowledge about the soil is more important today than ever before and more generally appreciated. Efficient farming depends essentially on suitable adjustments in plant-soil relationships, and rational land utilization is impossible without knowledge of the soil and its capabilities.

During the fiscal year 1936 the Soil Survey Division, in cooperation with local agencies, mapped about 20,000 square miles of rural lands in 31 States, Puerto Rico, and Hawaii. This work completed the survey of Puerto Rico and brought the total area covered to more than half the arable lands of the United States. The soil survey of Hawaii will be completed during the present fiscal year.

At the present time the Department is cooperating with the agricultural experiment stations of the seven States having an interest in the watershed of the Tennessee River which, in turn, are cooperating with the Tennessee Valley Authority for expediting the completion of a detailed soil survey of this region. This survey is absolutely essential in developing systems of agriculture for the improvement of the land and the protection of the reservoirs.

Information obtained from the survey of areas in Western States has permitted an extension in the acreage of certain special crops, and has indicated the areas where the accumulation of salts and the development of alkali would be a menace to irrigation projects.

Progress has been made in the development of a system for rating the various soil types according to their productivity for adapted crops and an increasing number of published soil surveys contain tables showing the inherent productivity of the soil as well as its productivity under different systems of management.

The Soil Survey Division prepared a special report on the characteristics and distribution of various kinds of organic soils and peat in the Pacific Coast States. This report paid special attention to the problems of soil conservation and flood prevention.

In July 1935 the Department issued C. F. Marbut's work, entitled "The Soils of the United States", which constitutes the final section of the Atlas of American Agriculture. This gives the accumulated results of the Department's soil surveys and brings into a focus the findings regarding soils as gained by Dr. Marbut and his associates during the last 35 years. It contains maps showing the areas covered by soil surveys up to June 1934, the distribution of the soil groups, the distribution of the parent materials of soils, and the distribution of soils without normal profiles.

An especially important feature is a large map of the United States in 12 sections showing the distribution of the country's soils according to 137 differentiated and 6 undifferentiated soil groups. There is also information on the classification of soils, their geographic relationships, their derivation and development, and their profile characteristics, as well as their physical properties and chemical composition. This report is the culmination of Dr. Marbut's life work.

Soil Chemistry and Physics

The Bureau of Chemistry and Soils is carrying on research on the chemistry and physics of soils to develop fundamental knowledge on composition and properties which has an important bearing on soil classification, soil conservation, and soil utilization, as well as on variations in the yield, composition, and food value of crops. It is also studying the causes for nonfertility of certain soils, the effects of arsenical insecticides on soils, and the value of peat as a soil amendment. During the past year several important publications have been issued as a result of these investigations. One of them, Technical Bulletin 484, presents analytical data for eight soil profiles, representing six of the great groups of soils, which show that the colloids of the great groups of soils differ from each other and that there exists a chemical basis for the characteristics of soils as manifested in the field. Another, Technical Bulletin 482, reports the results of studies on the occurrence of selenium in the soils of the United States. A second bulletin on this same subject is in process of publication.

Additional seleniferous areas have been found which produce toxic vegetation. Results of recent surveys indicate that toxic seleniferous areas are ordinarily found in certain geological formations. New areas where the soils are likely to be seriously seleniferous, judging from geological data, are now being explored. There seems to be no definite relation between the quantity of selenium in a soil and the quantity taken up by plants growing on it. The distribution of selenium in soils has been shown to be very widespread, and its primary source appears to be from volcanic activity. Its occurrence in small quantity in wheat appears to be world-wide.

Soils from the erosion experiment stations were studied with regard to the relationships between their physical constants. The same soils were examined by newly developed methods for certain elements which occur only in minute quantities and are not ordi-

narily included in soil analyses. Selenium, arsenic, copper, cobalt, nickel, zinc, barium, chromium, and vanadium were found in determinable quantities in each of the 11 profiles examined. The quantities varied from less than 0.1 part per million for selenium, cobalt, and nickel to as much as 708 parts per million for barium.

It is becoming increasingly apparent that these and other trace elements play an important role in soil behavior, as well as in plant nutrition and the food value of agricultural products. More exact knowledge concerning the chemical composition of soils, including their content of trace elements, will be essential in connection with a very comprehensive and fundamental cooperative research project that is being planned by the Bureau of Chemistry and Soils to determine the effects of soil, fertilizers, climatic conditions, crop rotation, cultivation, and variety of plant on the mineral and other constituents of plants and the value of plants for food purposes.

FERTILIZERS

Fertilizer studies demonstrated that the elimination of filler from fertilizers would save the farmers of the United States about $7,500,000 annually. It appears also that the purchase of double-strength mixtures, which can be manufactured without difficulty, would result in substantial savings. Nationally, the United States is self-contained as regards the principal fertilizing elements, and scientific research in this Department has contributed to the development of commercial fertilizer production. Interest is turning now to the comparatively recent recognition of the fact that mixed fertilizers should contain neutralizing agents to prevent the development of soil acidity. Research is advancing the production of fertilizer mixtures that are nonacid forming. One useful method is the use of ground dolomitic limestone.

Interest is growing also regarding the proper placement of fertilizers with respect to seed and plants, and the Department has developed a granulating process for mixed fertilizers to prevent the segregation of materials. Recent work on calcined phosphate indicates that the plant-food value of this product is as high as that of commercial superphosphate, and that the calcining process offers attractive possibilities for the production of phosphate fertilizer at low cost. A process has been developed in the Department for the production of potassium metaphosphate from potassium chloride and phosphoric acid. This product holds much promise as a fertilizer material because it consists almost entirely of potash and phosphoric acid and does not absorb moisture from the air. Also the Department has developed new compounds of urea with magnesium sulphate and magnesium nitrate which are useful for incorporating the secondary plant nutrient, magnesium, in fertilizer mixtures, as well as nitrogen.

New fundamental scientific knowledge has been acquired through basic research on the chemical and physical properties of elements and compounds contained in fertilizer materials, on the principles underlying catalytic action in industrial nitrogen-fixation processes, and on the fixation of nitrogen by living organisms and organic materials. The facilities of the Bureau of Chemistry and Soils for

modern physical and physicochemical research have been used to assist other bureaus of the Department having problems in this field. Thus, in cooperation with the Bureau of Plant Industry, the effect of X-rays on corn seed and tobacco plants was determined and spectroanalyses were made of the differences in the mineral elements content of toxic and nontoxic specimens of the roots of *Tephrosia* (*Cracca*) *virginiana* (devil's shoestring) which were under investigation as a source of insecticide.

Chemistry and the Farmer

Both hopes and fears cluster about the possibilities of chemical research and its bearing upon new uses for the products and by-products of the farm. Enthusiasts foresee important new markets and a quick solution of the whole farm problem. Warning voices say the chemist will synthesize foods in the factory and put the farmer out of his job. Industrial chemistry, they point out, has no particular preference for agricultural sources of raw material and may find what it wants elsewhere. Both the hopes and the fears should be discounted. There is no possibility either that chemistry will solve all the farmers' difficulties overnight or that it will do away with the need for farms.

The worth of a chemical discovery depends on the economic as well as the technical factors. Such things as cornstalks and cereal straw, for example, have some value as feed for livestock and as fertilizer. It pays the farmer to sell them for industrial utilization only when he receives more from their sale than they are worth to him as feed and manure. After the chemist has demonstrated that an industrial use for a farm product is possible, the manufacturer must test its commercial feasibility. Also, the farmer should remember that the development of new uses for one of his products may hurt the market for others.

In like manner we may discount the fears generated by the progress of industrial chemistry. Chemists have synthesized a small number of organic compounds formerly obtained from plants, but man must still apply to nature direct for food, clothing, and shelter. Probably agriculture will always have to produce most of the food substances that man requires, most of the clothing materials, and a good part of the materials required in providing shelter. In any case the change of emphasis is not likely to be appreciable in the near future. For as far ahead as we can see, chemistry will aid and not supplant the farmer.

There is, however, a side of the industrial-utilization problem which should be considered carefully. Chemical discovery, like other aspects of technical progress, is not necessarily an unmixed blessing, particularly to the farmer. If it opens new possibilities, it creates also a need for readjustment, especially when it affects intercommodity competition. For example, the utilization of sugarcane bagasse in the manufacture of rayon may diminish the demand for cotton. Soybean-oil production, stimulated by a demand for soybean products in the automobile industry, may come directly into competition with cottonseed and other vegetable oils. Sometimes, too, the devel-

opment of new uses for farm products attracts more people into farming and disturbs the balance between town and country.

Such considerations should not deter chemical research, for science cannot foresee all the probable consequences of its discoveries. That is beyond human wisdom. But the exploitation of particular products is not the only thing to keep in mind. Success in that direction will inevitably benefit some groups more than others, and public agencies engaged in chemical research should cooperate with other branches of the public service in promoting the most nearly equitable distribution of the benefits. There is special need for the collaboration of chemists and economists.

This Department endeavors simultaneously to promote the interests of producers, manufacturers, and consumers, because it is interested not only in the production but also in the commercial utilization and final consumption of agricultural commodities. While the work of the chemist in creating new uses for farm products may temporarily benefit some lines of production to the disadvantage of others, the Department believes the final balance will usually be in favor of the farmer.

It is important to prevent the unscrupulous exploitation of producers or would-be producers on false grounds. There are opportunities in parts of the United States for the culture of the tung tree. But land unsuited to that purpose is being sold to gullible investors. The same thing has happened in the case of hemp; and the sale of land is not the only means of diverting technical progress to improper ends. Everyone should understand that hard-headed cost accounting and commercial research are necessary to get the best results and that the laboratory discovery is only the first step, which may not be followed for a long time by the final demonstration on a commercial scale. In the files of this Department are recorded scores of chemical discoveries and innovations, which, though technically successful, remain unutilized commercially for years because the original costs were too high. For example, the Department developed a process, using dilute nitric acid as the pulping agent, for making high-grade cellulose from bagasse. But it was not until ways had been found to cheapen the production of the acid that the process became commercially practicable. Premature exploitation of research findings is a constant source of loss to investors and producers.

UTILIZATION OF DAIRY BYPRODUCTS

Investigations in the Bureau of Dairy Industry to develop ways to utilize whey or its separate constituents more efficiently have given promising results. The whey produced annually in the United States, as a byproduct in the manufacture of cheese, contains about 300,000,000 pounds of milk solids. Yet whey is commonly wasted or used only in limited amounts as feed for pigs and poultry. Dairy investigators have long considered this practice inefficient. They regard the feeding of whey to livestock as justifiable only until better methods of producing human food from whey can be developed.

Whey contains nearly half the food solids of milk. It contains all the valuable sugar and at least one vitamin, so that it possesses exceptional nutritive properties. Yet it has found few uses as

human food because it has no pleasing taste itself, and no special ways have been developed heretofore for using it. Within the last year the Bureau has found that whey may be used to enrich a variety of food preparations by taking advantage of its chief distinguishing characteristic, which is its lack of casein.

Casein is the substance that causes coagulation in milk under high temperatures or in the presence of acid vegetables or fruits. Manufacturers of vegetable soups can use condensed whey, whey powder, or whey cream in place of normal milk or cream to enrich their products. The whey solids will cause less difficulty with coagulation, the soups will retain their natural color better, they will have the characteristic milk flavor, and a greater nutritive value than soups made without milk solids.

The solids can also be combined with highly acid fruit juices, such as orange, grapefruit, strawberry, and similar fruits. Because of the high acidity of the combination little heat is required for sterilization, and these beverages and whips may be canned without a cooked flavor. By varying the combinations, sterilized whips, fruit drinks, and mixes suitable for freezing in a mechanical refrigerator can be made available to the housewife. These are probably only a few of the ways in which whey solids may be combined with other materials to improve old or create entirely new food products.

Young pigs will grow satisfactorily on pasture supplemented with whey, but it is often a problem to adjust the supply of whey to the requirements of the growing pigs. In the flush season there is likely to be a greater supply of whey than the pigs can consume. The Bureau's investigations indicate that surplus whey can be acidified with an active lactic-acid culture and concentrated at the factory to make an acid product that can be held until it is needed for feeding. Also, to provide for feeding roughage and whey when pasture is not available, concentrated sweet whey may be mixed with grass or alfalfa and ensiled. Preliminary trials show that pigs will consume this ration and make satisfactory growth.

Information developed in the Bureau's laboratories has found expression in a number of new commercial ventures. Cheese of the Roquefort type is now being made by a small factory which uses an abandoned coal-mine shaft for a curing room. The ideal natural temperature and humidity conditions of the shaft eliminate the necessity of providing artificial curing conditions. Arrangements have been made to start a similar operation in which a natural cave will provide the right conditions for curing. In one factory, with rooms artificially cooled and humidified, the Bureau's method for manufacturing a soft cheese of the Italian Bel Paese type has been established. A dairy-byproducts company has built and is successfully operating a factory for the manufacture of lactic acid by fermenting whey. A large volume of whey is being utilized.

Experimental shipments of concentrated frozen milk have been made to the Canal Zone under the Bureau's direction, to determine the feasibility of providing fluid milk in the Tropics, on shipboard, and in other places where good-quality milk is unobtainable or the supply is inadequate. Research in the Bureau has demonstrated that milk may be concentrated to one-third of its volume, or less, held at

temperatures below freezing for weeks, and then brought back to its original volume by adding water, without losing the characteristics of fresh clean-flavored milk.

ANIMAL INDUSTRY

Superior types of livestock continue to be one of the most promising means of increasing the efficiency and economy of production. Great variation in the growth of pigs, similar in outward appearance, has occurred at the National Agricultural Research Center, Beltsville, Md. Under the conditions of management and on identical rations, pigs of the same litter varied as much as 100 days in the time required to attain a weight of 225 pounds. And within the same breed the quantity of feed required by different litters to make 100 pounds of gain varied from 325 to 500 pounds. Such observations indicate the feasibility of selecting the breeding hogs that are naturally fast and economical growers. There are indications also that rapid growth is associated with tenderness in meat.

Studies with Danish Landrace hogs imported a few years ago have now reached a stage to permit comparisons with American-bred hogs. When the chilled, dressed carcasses of 40 Landrace hogs and 36 of 2 American breeds were compared, the former had the higher percentage of ham, loin, and bacon and lower percentages of picnic shoulder and head. The higher yield of bacon in the Landrace hogs is especially noteworthy. In general, the Landrace hog excelled in the production of the more valuable cuts of pork.

In the study of more efficient cattle production, the Department has sought a type of animal that will produce beef profitably under adverse conditions of heat and insect pests. Such cattle are especially needed in the Gulf coast region and in other sections having a similar climate.

Crosses between Brahman cattle and several beef breeds already established in the United States have given promising results. Cross-bred types developed from the Guzerat (Brahman) and the Aberdeen Angus breed have shown high adaptability to semitropical conditions. The second generation of calves carrying three-fourths Aberdeen Angus blood and one-fourth Guzerat have, in all instances, been polled and black. A noteworthy result is the increased weight, at weaning age, of cross-bred calves over purebred Aberdeen Angus calves. First crosses, containing 50 percent of the blood of each breed, averaged 455 pounds, whereas Aberdeen Angus calves averaged 391 pounds. Second-cross calves, possessing three-fourths Aberdeen Angus and one-fourth Guzerat breeding, averaged 491 pounds at the same age. These results are in the direction of improvement both in adaptability to the region and in desired market characteristics.

Other breeding studies have been supplemented with tests on the tenderness of the resulting meat. Four years' experimental work has shown that roasted rib cuts from grade Hereford cattle were more tender than corresponding cuts from cattle of native breeding slaughtered at the same age. These studies indicate the presence of hereditary differences in fat distribution and tenderness.

In a comparison of methods of wintering cattle under western-range conditions experiments showed wide differences in costs. When breeding cows were kept on reserved creek bottom and allowed to graze sagebrush range supplemented by 83 pounds of cottonseed cake per cow, the wintering cost per animal was $2.84. The cost of wintering similar cows on alfalfa hay at the rate of 765 pounds per head was $4.51. Experiments of this kind indicated the economies possible by altering systems of management. When applied to large herds of cattle, even small differences of the kind cited result in large savings and impressive net profits.

A valuable scientific aid in sheep breeding and in the raising of other animals for hair or fur is a device recently developed in the Department's animal-fiber research laboratory. The instrument makes possible the procurement and study of very thin cross sections of fiber in a few minutes' time. The various characteristics of fiber associated with suitability for commercial purposes are readily observed by the use of this device. Already it is being used in many fields of industry. Still another instrument developed in the same laboratory during the year makes possible the measurement of length and crimp of wool and hair fibers in a more accurate and efficient manner than with previously available equipment.

Foreign Breeds Introduced

In connection with improvement of animal types the Department has obtained from various foreign sources species and breeds of livestock having noteworthy characteristics. Such stock, introduced in 1935 and 1936, includes Nonius horses and Puli sheep dogs from Hungary, red Danish cattle from Denmark, and south Devon cattle, large black hogs, white Austrian turkeys, and White Wyandotte chickens from England. After receiving veterinary inspection and meeting other quarantine safeguards these animals were admitted to Department experiment stations for breeding and feeding studies and related observations. To some extent also they are being used in cross-breeding experiments with selected types raised in the United States.

Security From Livestock Diseases

Each year the livestock industry of the United States becomes more secure from diseases, parasites, and other pests. Through methods supplied by scientific research, stockmen and their veterinary allies have recently extended the frontiers of animal health very materially. A brief appraisal of the animal-disease situation at the end of the last fiscal year indicates several noteworthy advances in this field.

Bovine tuberculosis has been practically eradicated from 40 of the 48 States in the Union and from 95 percent of all the counties. There is considerable need, however, for continued retesting of herds to locate and eradicate any remaining infection. Cattle carcasses which, because of tuberculosis, failed to pass Federal inspection at the principal livestock markets numbered less than 10,000 in 1936 as compared with more than 28,000 the previous year. Condemnations of parts of cattle carcasses likewise were much less, being about half as many as during the previous year. A reduction in tubercu-

losis, though in less degree, was observed also in swine. These figures, based on official veterinary inspection of millions of animal carcasses, signify a large saving of meat as well as an unmistakably improved condition in the health of cattle and swine.

Extensive public interest in the elimination of Bang's disease, or infectious abortion, has caused the Department to continue the testing of cattle in cooperation with State officials and livestock owners. Agglutination blood tests for the detection of this disease were applied to approximately 6,600,000 cattle. About 7 percent were reactors as compared with 11 percent during the preceding year. The elimination of Bang's disease, which has in the past caused heavy losses and much discouragement in cattle breeding, has resulted in greater optimism among dairymen and others whose herds have thus been placed on a more secure health basis.

In search of an improved diagnostic agent for the identification of cattle affected with this disease, the Department recently developed a biological product known as a stained antigen for the purpose. This product makes possible a rapid whole-blood test, which has several practical benefits over the present slower and more expensive methods of diagnosis. A thorough field trial of the new method was begun by the distribution of sufficient stained antigen for testing 13,000 cattle under Department supervision.

In the eradication of the cattle fever tick the area in continental United States still under Federal quarantine has been reduced to only 9 percent of its original size. The sections still infested with ticks are confined to parts of three States—Florida, Louisiana, and Texas—in contrast to infestation of 15 States when the work began in 1906. Systematic eradication of cattle ticks was recently begun in Puerto Rico.

Control of hog cholera has reached the point where immunization by the serum-virus treatment, developed by the Department, is largely a routine procedure. The method is widely known; serious outbreaks of the disease are infrequent; and the Department has largely relinquished direction of control work to the States. However, it continues to supervise the preparation and distribution of the virus and serum, of which a total of more than 500,000,000 cubic centimeters was produced last year under Federal licenses. As a means of assuring adequate production of these products for possible emergencies, the Department has aided manufacturers in perfecting a marketing agreement directed toward this end.

A New Immunizing Product

As a still further measure of hog-cholera control, the Department recently developed a new immunizing product. Known as crystal-violet vaccine, this product has given distinctly encouraging results in experimental trials. It has provided approximately 99 percent satisfactory protection and has several advantages, including greater safety, over the familiar serum-virus method of immunization. During the last year commercial production of the vaccine on a small scale was sanctioned by the Department in order that this new product might be thoroughly tested under various field conditions. Until the merits of the vaccine are more thoroughly established, however, reli-

ance must still be placed in the serum-virus treatment, the efficacy of which, when properly administered, has been fully established. A present limitation of the crystal-violet-vaccine method of immunization is its slowness in furnishing protection. Immunity does not appear to be established usually until at least 2 weeks after a hog has been vaccinated.

The drought of 1934, with resulting extensive shipments of livestock, retarded several lines of livestock disease-eradication work. Some spread of scabies in cattle and sheep occurred in Central and Western States, but scabies of horses now appears to have been eradicated, inspections revealing no cases during the year. The eradication of the horse disease, dourine, likewise appears to be virtually accomplished, but State authorities are continuing the quarantine of a few areas where the presence of the disease is suspected. Any remaining infection is considered to be very slight, judging from the evidence of only one animal giving a positive reaction to this malady within the last year.

A comparatively newly identified disease of horses and other equines has caused anxiety as well as serious loss in several localities. Known as infectious encephalomyelitis, and occasionally by such nonspecific terms as blind staggers, brain fever, and sleeping sickness, this malady has appeared in no less than 20 States. It is caused by an infectious virus which produces nervous symptoms resulting from inflammation of the brain and spinal cord. The mortality is high, and in animals that recover there may be permanent impairment of the brain. Outbreaks occur chiefly during the summer and fall months and in low-lying and moist areas. The use of a specific serum has been helpful in preventing the spread of infectious encephalomyelitis, but it produces only a short-lived immunity. The Department is studying the disease and testing various biological products and drugs reported as being beneficial for its prevention or treatment.

Anthrax caused comparatively slight loss during the year, no serious outbreaks being reported to the Department. Assistance in preventing the disease was given to Indians on reservations where outbreaks occurred several years ago. The horse disease, glanders, which at one time caused heavy losses, has been practically eradicated.

Recent research has disclosed several highly effective methods of combating injurious internal parasites, such as kidney worms of swine and liver flukes of cattle and sheep. Livestock owners have been quick to adopt and apply the Department's recommendations. In several instances supplementary benefits derived have greatly exceeded the original purpose of control methods.

For instance, Department investigators have shown that drainage of wet, marshy, and boggy pastures is the most practical procedure for controlling liver flukes. In several areas these parasites were killing as many as 50 percent of the sheep and stunting or killing calves. The broadcasting of copper sulphate to destroy the snail intermediate host is, at best, only a temporary expedient and must be continued from year to year in order to insure the destruction of the fresh crops of snails which reappear sooner or later. Drainage, on the other hand, is an effective bulwark against aquatic snails, which invariably perish on dry land. Recently reclaimed boggy meadows contained thousands

of dead snails, many of which were the potential and actual conveyors of the liver fluke that is deadly to sheep and injurious to cattle as well as to several species of wild animals.

But besides controlling liver flukes, the drainage of wet pastures has produced a marked change in the type of vegetation. The coarse aquatic grasses containing little or no nourishment for livestock gradually disappear as the pastures become dry; and, as a result of natural seeding, highly nourishing forage, including clover, timothy, and other nutritious plants, take their place. This results in a permanent improvement of the land; and, with reduced water in the soil, the land produces good forage earlier in the spring and later in the fall.

In the Western States where liver-fluke control is in progress drainage of marshy meadows makes considerable water available for irrigation. In Utah, particularly, the water from the drainage ditches is being diverted into irrigation canals, thereby adding materially to the supply of water available for irrigation. Incidentally drainage of wet and boggy lands has considerable value as a mosquito-control measure.

In short, the control measures for liver flukes are not only effective in reducing serious losses in sheep and stunting in cattle but are also of marked value in converting submarginal lands into productive pastures, adding to the available water supply of areas dependent on irrigation, and aiding in the control of mosquitoes.

Pullorum disease, a major drawback to poultry raising, is being controlled by progressive flock owners through the use of the rapid whole-blood test developed by the Department a few years ago. Commercial production of the stained antigen used last year in making the test was sufficient for testing more than 10,000,000 fowls. Under the provisions of the national poultry improvement plan thus far adopted by 34 States, the Department approves the quality of all this antigen used in official testing, thus insuring a high quality of this diagnostic agent.

Besides these advancements in curbing losses from livestock diseases, the Department has continued its quarantine and inspection services against the possible introduction of infection from abroad. During the year the United States remained entirely free of foot-and-mouth disease, rinderpest, surra, contagious pleuropneumonia, and other maladies that cause heavy losses to livestock owners in some foreign countries.

The increase of about 7 percent in enrollment reported by the 10 federally accredited veterinary colleges of the United States augurs well for continuing the foregoing measures for the protection of the Nation's livestock.

Supervision of Livestock Marketing

Supplementing its regulatory work of veterinary character, the Department has sought to improve conditions of livestock marketing. Several noteworthy developments of the year resulted from procedures under the Packers and Stockyards Act.

Three cases involving orders of the Secretary which prescribed reasonable commission rates and stockyard charges at Chicago, Ill., and St. Joseph, Mo., were upheld by the United States Supreme

Court. As a result legal action has been taken in the lower courts for the return of excess commissions and stockyards charges to shippers. The amount of such returns involved probably will exceed $1,000,000. The decisions of the Supreme Court were important and significant in that they sustained procedures followed by the Department in determining stockyard charges and commission rates.

Congress amended the Packers and Stockyards Act during the year to include the supervision of poultry marketing in a manner similar to the supervision of the marketing of other classes of livestock. The amendment provides for the licensing of persons engaged in furnishing facilities or rendering services for marketing live poultry in interstate commerce in cities designated by the Secretary of Agriculture. The regulation of rates and practices of licenses is a further provision of the amendment.

Investigations of the poultry-marketing situation, together with requests for supervision from a number of cities, resulted in the designation of poultry markets in 15 cities as being subject to Department supervision, up to the close of the fiscal year 1936.

FORESTRY

Most people have regarded forestry as largely a means of assuring an adequate future supply of timber, and it should, of course, be valued for that purpose. Four-fifths of our commercial forest land, and at least 90 percent of its potential productivity, are in private ownership; and private ownership has not generally endeavored to maintain a continuous timber harvest. It is extremely important, therefore, to promote sustained-yield practices on the publicly owned forest land and to encourage such practices on the privately owned land. Sustained forest production is essential for the general welfare. But forestry has other ends as well, notably the conservation of soil and of water—in other words, the prevention of erosion and of floods. Fortunately, the methods which conserve timber productivity at the same time promote the other objects of scientific forestry so that no conflict arises. Curbing forest exploitation is good for the timber industry and also for the public interests that depend upon the forests. This Department recommended, and Congress in part approved during the last year, a program for coping with some of the responsibilities involved.

That a common interest extends to all forest lands and that private, as well as national, forests ought to be managed on a sustained-yield basis is now generally acknowledged. There is a public, as well as a private, obligation. Accordingly, fire protection by the Civilian Conservation Corps under the direction of the Forest Service is under way on private, as well as public, forest lands. The expenditure on private lands for this purpose has already exceeded $58,000,000. For the current fiscal year Congress has appropriated increased funds for forest-fire protection by Federal agencies in cooperation with the States and with private owners. Forest research carried on by the Forest Service similarly benefits public and private land ownership, through its influence on the utilization, as well as the production, of timber.

Federal acquisition of forest lands through purchase was first authorized in 1911, national forests previously having been set aside only from the western public domain. Prior to 1933, however, the Federal acquisition of forest lands never exceeded 550,000 acres in any one year. The total area approved for purchase was only 4,727,680 acres in the first 22 years of the program. In 1933 Congress authorized accelerated activity, and the area acquired in the 3-year period ended June 30, 1936, exceeded 11,400,000 acres. The acquisitions in the last fiscal year aggregated 2,998,060 acres. Besides adding to the system of federally owned and managed national forests this accelerated program assured county governments of future revenue from lands that might otherwise have been tax-delinquent, and harmonized with other aspects of the national agricultural policy. The national forest system now covers more than 170,000,000 acres in 37 States and 2 Territories.

Advantages resulting from the Federal ownership and multiple-use management of forest lands are substantial and varied. They include protection to watersheds, conservation of merchantable timber, scientific management of more than 83,000,000 acres of livestock range, preservation of wildlife, particularly big game and fish, provision of recreational facilities, and soil and water conservation, with resulting benefit to power development and irrigation. They afford innumerable opportunities for recreation; more than 17,000,000 persons visited the forests last year for rest and relaxation. Administered by the Forest Service under a system of coordinated use, our national-forest resources furnish support directly to more than 1,000,000 persons. Modern forestry thus includes more than producing continuous crops of timber. It comprises the planned management of forest, range, and wild lands, and of their many resources; it has to do with conservation through the use of organic resources and services in the interest of general welfare.

Forest Protection and Flood Control

How important it is to protect forest, range, and other vegetative cover so as to retard the water run-off and prevent erosion becomes evident when floods occur. For example, Pickens, Frankish, and San Dimas are mountain canyons opening out into fertile valleys of southern California. Fire denuded 5,000 acres in Pickens Canyon in 1933. Fire similarly swept Frankish Canyon in 1935. Fire did not visit San Dimas Canyon. On New Year's Day 1934 a flood swept out of Pickens Canyon, destroyed 200 homes, and killed 34 persons. Though the same storm hit nearby San Dimas Canyon, it caused no flood there. This year in January and February floods swept out of Frankish Canyon through the cities of Upland and San Bernardino. Though the same storm struck the unburned San Dimas Canyon, it did not precipitate a flood there.

Near Centerville, Utah, in 1930 overgrazing was the primary cause of a flood which wrecked homes and buried orchard lands under soil, rock, and debris. There was no flood from a nearby watershed that had been properly grazed. Floods come less frequently and have lower crests where a vigorous vegetative cover remains.

Reservoirs and distributing systems that carry water to some 20,000,000 irrigated acres had a value in 1930, according to the census, of more than $1,000,000,000. Many billions have been spent for downstream engineering to control floods that start with small streams and additional sums for removing silt from navigable waterways. The Federal Government has incurred most of this expense. Yet it has invested less than $70,000,000 to purchase lands where floods and erosion begin, and less than $14,000,000 for replanting denuded forest and range lands. One of the best and cheapest ways to prevent soil erosion and combat the danger of floods is to reclothe denuded slopes with forest and other vegetative cover. In dealing with the flood problem, prevention is better than cure.

As a flood-prevention measure, the Federal acquisition of 81 million acres of lands on important watersheds in 27 States east of the Rocky Mountains has been recommended. Such lands should be protected, revegetated where necessary, and administered as parts of our existing national forests. The Forest Service has outlined an expanded program and recommended it to Congress. Preventive measures in foothills and mountains will help to conserve investments already made in downstream engineering. Without such preventive measures the work downstream may not have much effect.

In the fall of 1934, following the great drought of that year, the Forest Service began to plan shelterbelts in the Great Plains. Such shelterbelts serve as barriers against soil drying and wind erosion. They help to catch and retain snow, and to delay the surface run-off. The shelterbelt planting was not started until the problem had been thoroughly studied, surveys made of existing shelterbelts, and analysis completed of 25 years' experimental work by Federal bureaus and State agricultural colleges. By agreement with farmers, the Forest Service planted about 7,000 acres in the spring of 1935. This year it planted nearly 24,000 acres, using 23,000,000 trees in the work. Examinations in June of all the plantings revealed an average survival of 81 percent, a highly satisfactory figure for any forest-planting operation. However, Congress decided to discontinue the Plains shelterbelt project and appropriated $170,000 to conclude the work and to dispose of the trees still remaining in the nurseries.

Report on Range Resources

In response to Senate Resolution 289 (74th Cong., 2d sess.), this Department made a special report on the original and present condition of our range resources. The report was prepared by the Forest Service. As required by the resolution, it dealt with the factors that have led to the present condition of the range, with the social and economic importance of range use and conservation, and with methods for restoring its productivity. Various Federal and State agencies furnished data for the report.

The western range is much larger and more important to the national welfare than most people realize. It includes some 728 million acres, or nearly 40 percent of the total land area of the country. It is the mainstay of a 4-billion-dollar western livestock industry, and includes four-fifths of the principal water-yielding areas on the watersheds of major western streams. Low precipita-

tion makes water the limiting factor in nearly all western development.

In the range country in 1930, according to the census, there were 775,745 farm units and nearly 400,000,000 acres of land in farms. Normally these farms grow 35 percent of the feed for western livestock. Except for highly specialized crop farming, mostly on irrigated land, western agriculture is primarily an integration of range-livestock grazing and crop farming.

Forage depletion for the entire range area averages more than 50 percent—the result of a few decades of livestock grazing. Range depletion on the public domain and grazing districts averages 67 percent; on private lands about 50 percent. Seventy-six percent of the area is still on the downgrade. No less than 589 million acres of range land is eroding more or less seriously, reducing soil productivity and impairing watershed services. Three-fifths of this area is adding to the silt load of major western streams. An outstanding cause of range depletion has been excessive stocking. Some 17.3 million animal units are now grazed on ranges which it is estimated can carry only 10.8 million.

Severe recurrent drought has contributed to this overstocking. Stockmen have been forced to damage the range, in order to meet their immediate obligations. Unsuitable land laws have made the range a bewildering mosaic of different kinds of ownerships and of uneconomic units. Most spectacular among the maladjustments of range-land use has been the attempt to use more than 50 million acres for dry-land farming. About half of this area, ruined for forage production for years to come, has already been abandoned for cultivation.

The national forests furnish indispensable summer range. The 83 million acres grazed by domestic livestock has improved so that it is now depleted only 30 percent; important water-yielding areas on national forests are being afforded proper watershed protection and it has been necessary to exclude livestock from only a comparatively small area. Research carried on by the Forest Service is showing how to manage range lands for stable forage and livestock production, how to reseed severely overgrazed range and abandoned dry farms in the range area, and how to coordinate grazing use with erosion prevention, flood control, and water delivery, tree reproduction, wildlife, and recreation.

PLANT RESEARCH

Excellent results continue to be secured with the two outstanding varieties of upland cotton introduced and developed by the Bureau of Plant Industry. These varieties are Acala and Lone Star. These two cottons, with the strains and varieties developed from them, are now annually planted on more than 1,000,000 acres in the Cotton Belt, distributed from Georgia to California. Practically the entire upland cotton acreage in the irrigated valleys of the Southwestern States—Texas, New Mexico, Arizona, and California—is planted to Acala. Because of its productiveness and superior quality of fiber, Acala has become outstandingly popular with growers in parts of Oklahoma and Arkansas, and in test plantings conducted for several years at State

and Federal stations in Texas, Acala has been shown to be especially well adapted to the great blackland soil area of that State.

One of the outstanding results of the past year's work concerns the Hopi cotton, a small-boll type grown, probably for centuries, by the Hopi Indians in northern Arizona. This cotton has a staple only thirteen-sixteenths of an inch long, but fiber studies and spinning tests conducted by the Bureau of Agricultural Economics show that it approaches sea island in fineness and produces a yarn as strong as that made from $1\frac{5}{32}$-inch upland cottons. The $1\frac{1}{8}$-inch fiber from a first-generation cross between Acala and Hopi produced a yarn as strong as that derived from $1\frac{1}{2}$-inch upland cotton.

Interest in sea-island cotton has greatly increased, both among former growers and among manufacturers desiring this finest of the world's staples for special textile purposes. In spite of the many hazards of production under weevil conditions in the Southeastern States, about 700 acres were planted in 1935 in northern Florida. Seed for this acreage was the increase from a small reserve stock furnished by the Bureau in 1934, through the Florida Extension Service, to a few growers for experimental demonstrations. Only 15 bales were produced on the 175 acres planted in 1934, but 170 bales were produced on the 700 acres planted in 1935, and sold at prices ranging from 25 to 28 cents a pound. As a result of the more favorable returns in 1935, about 4,000 acres were planted in northern Florida and southeastern Georgia in 1936.

The need for developing earlier and more prolific strains of sea island or a substitute for this cotton better adapted to present conditions has become acute. Special studies are being made, therefore, of hybrids between sea island and outstanding upland long-staple varieties to find a type combining the long, silky quality of sea-island fiber with the larger bolls and earlier maturity of upland. Approximately 8,000 hybrids were made in 1935, about 3,000 of these being sea island crossed on upland and 5,000 upland crossed on sea island. A system of convergent crosses, in which hybrids are back-crossed to one or both parents, is being used in an effort to establish pure strains having the desired combinations of fiber quality and plant characteristics.

Among the extra-staple upland cottons showing special promise as a substitute for sea island is a selection out of the Tidewater variety developed by a former sea-island breeder near Charleston, S. C., in cooperation with specialists of the Bureau. The new strain is much more productive than sea island, has bolls about twice the size, and produces a fine quality of fiber $1\frac{1}{2}$ inches long. The stock is being further selected and used in the hybridization work with sea island. Improved strains of Meade, an early upland variety, with fiber similar to sea island in length and quality, are also being developed for use in the studies of extra-staple cottons adapted to production in the Southeastern States.

The most important result in Egyptian-type cotton breeding during the past year is the establishment in commercial production of the SxP variety, derived from a cross between Sakel, the longest in staple of the Egyptian varieties, and the Pima variety of Arizona. Approximately 1,700 acres of SxP were grown in the Salt River Valley

in 1935, and the yields were so satisfactory and the market for the product was so active that the demand for planting seed in 1936 greatly exceeded the supply. Some 10,000 acres of this variety are being grown in 1936 in the Salt River Valley and neighboring districts. Production on this scale should determine definitely the position of this cotton in the markets as compared with that of Pima. If SxP can be substituted satisfactorily for Sakel cotton, large quantities of which are imported annually into the United States, a considerable expansion of the acreage of Egyptian-type cotton in the Southwest would be likely to result, and increased production should place the American-Egyptian industry upon a more stable basis.

Grains

The stem rust epidemic of 1935 was perhaps as severe as or even more so than those of 1904 or 1916. Late seeding in the spring wheat belt, delayed maturity of winter wheat in Kansas and Nebraska following late germination due to a dry fall and winter, a rank growth of wheat late in the season, unusually favorable conditions for the development of the rust, and an abundance of inoculum from the wheat fields of Texas, combined to produce the most widespread epidemic in the history of the Great Plains. The loss in North Dakota alone has been estimated at more than $100,000,000 and losses were proportionately as great in South Dakota and Minnesota. The winter wheat crop also suffered though not to so great an extent.

The Thatcher variety of wheat, produced as a result of research by this Department and the Minnesota Agricultural Experiment Station and distributed to farmers last year, withstood the epidemic remarkably well. Nominal damage only was suffered by this variety as compared with complete or nearly complete failure for the Marquis variety under similar conditions. Ceres, which is somewhat resistant to rust, was also severely injured, though not to so great an extent as Marquis. Thatcher has proved acceptable to the grain and milling trade and popular with farmers. The acreage is being rapidly increased.

Three other new varieties of wheat, produced as a result of the cooperative work of the Bureau, have recently been distributed to farmers. Rex, produced at the Moro and Pendleton, Oreg., field stations, was first grown commercially in 1934. Several thousand acres were seeded for the 1936 crop. The chief characteristics which commend this variety to farmers are its resistance to the principal races of bunt occurring in the Pacific Northwest, early maturity, winter hardiness, stiff straw, resistance to shattering, and high yields. It is recommended principally for the area south of the Snake River in Washington and Oregon.

Hymar, produced at the Washington Agricultural Experiment Station, is also highly resistant to the races of bunt most generally prevalent in the Pacific Northwest. It is popular with farmers chiefly because of a relatively high test weight and high relative yields with favorable conditions with respect to moisture. It is grown chiefly in the Palouse area of Washington north of the Snake River.

The quantity of water in the soil at seeding time is definitely related to the yield of winter wheat. Recent analysis of soil-moisture and crop-yield data obtained in experiments extending over a period of 26 years in the central Great Plains has developed principles by which the farmer may recognize at seeding time conditions that indicate high probabilities of failure or success and regulate the seeded acreage accordingly. The depth to which the soil is wet can be determined by observation, and is a good measure of the quantity of water in the soil. The prospect of a good crop increases with the depth to which the soil is wet. When wheat is planted in a dry or nearly dry soil, the probability of success is extremely low. At three stations in western Kansas the chances were 71 out of 100 that the crop would be a failure (4 bushels or less per acre), and there were only 18 chances in 100 of producing a 10-bushel or better yield. When the soil was wet to a depth of 3 feet at seeding time, the chances of failure were reduced to 10 in 100 and the chances of producing a 10-bushel or better crop were 84 in 100.

When little or no rainfall occurs soon after seeding in soil moist to a depth of only a few inches, the probability of failure is greatly increased. When the initial soil moisture is deficient and the precipitation is low to April 1, it is probable that abandonment of the crop and the conservation of water in a summer fallow for a future crop will pay far better than allowing the water to be wasted by the poor crop and the weeds on the land.

Much of the hazard of winter-wheat production in the central Great Plains can be avoided by limiting the acreage in years when wheat must be planted on soil that is not wet to an adequate depth. In some sections a summer fallow for an entire season may be necessary to store the necessary quantity of water, and in sections with heavier precipitation cultivation beginning immediately after harvest may be sufficient in most seasons. In particularly dry seasons no method of cultivation may be able to provide the necessary protection.

Fifteen varieties of oats, developed by breeding mostly in cooperation with the Iowa, New York, Oregon, and Idaho Agricultural Experiment Stations, were distributed from 1913 to 1931. These improved varieties are now grown on 10,000,000 to 15,000,000 acres annually. Among these varieties Richland and Iogold are highly resistant to stem rust, and Markton is extremely resistant to smut. These varieties have been crossed with others resistant to crown rust, and certain of the hybrid selections from the crosses are resistant to all three diseases and in addition are very promising in yield.

Eleven corn hybrids developed in cooperation with the Iowa, Illinois, and Indiana Agricultural Experiment Stations were distributed during the period from 1932 to 1934, inclusive, and were grown on nearly 115,000 acres in 1935. Each of these hybrids has yielded an average of 12 to 26 percent more than good local varieties in comparative tests during the last 4 or 5 years. These hybrids also have been much more resistant to lodging than the open-pollinated varieties with which they have been compared.

Experiments with newly developed early maturing varieties, such as Sooner milo, indicate that they may be planted as late as July 1 or 15 in most of the commercial grain sorghum producing areas and still

mature a crop of grain. For late planting, certain of these newly developed varieties are far superior to the ordinary varieties that are more productive when planted early. Sooner milo has matured and yielded satisfactorily as far north as South Dakota, and also under irrigation at Logan, Utah, in the intermountain region.

The root-rot disease attacking milo and darso has been found to be caused by the organism known as *Pythium arrhenomanes* Drechs. This organism occurs in the soil of many localities and attacks corn and sugarcane and certain varieties of sorghum. This disease can be controlled by the use of resistant varieties. Resistant strains of milo have been selected by the Kansas Agricultural Experiment Station in connection with cooperative studies of the disease. Susceptibility to the disease is inherited in a simple genetic manner.

The "white-tip" disease of rice has been demonstrated to be caused by an iron deficiency. The disease is characterized by a loss of chlorophyll from the leaf tips and by chlorotic spots in older leaves. Plants severely affected have dwarfed, twisted culms and twisted leaves and panicles, a condition that results in a marked reduction in yield. Some varieties are less susceptible than others. In greenhouse experiments the deficiency of iron, which is associated with an alkaline soil condition, was corrected by applications of calcium cyanide, sulphur dust, or ammonium sulphate.

Grass and Pasture

Ecological studies in the central and southern Great Plains to determine the effect of heat and drought on native grasses were made at eight different stations in this region in cooperation with the Kansas Agricultural Experiment Station, and the Division of Dry Land Agriculture, and the Soil Conservation Service of the Department. Buffalo grass and blue grama constituted more than 90 percent of the total vegetation on all soils except those which were very sandy. Buffalo grass was more abundant than any other grass on the heavier soils, but blue grama was found to be adapted to a much wider range of soils. A large percentage of the native grasses were killed during the drought in 1933–34. Soil blowing and overgrazing contributed materially to the damage, but heat and drought caused much more injury than grazing. As the intensity of grazing was increased the actual ground cover of buffalo grass decreased. Heavy grazing and drought caused more injury to blue grama than to buffalo grass. Pastures were severely injured by the drought but surviving plants remained evenly distributed so that with favorable climatic conditions and proper management recovery to normal stands should be possible in a few years.

Woolly fingergrass introduced from South Africa was grazed for the first time at Tifton, Ga., in comparison with other grasses. This grass, planted vegetatively in 1934 on unfertilized Tifton sandy loam soil and with an incomplete stand, carried for 216 days three head of steers with an initial average weight of 443.3 pounds. The average gain per steer was 340.3 pounds or a daily average gain of 1.58 pounds per head. This was the largest daily gain on any grass pasture at Tifton, and these steers were in better condition than any others. Comparable steers on a pasture of carpet grass, Dallis grass,

lespedeza, and white clover fertilized annually with 600 pounds per acre of complete fertilizer made an average daily gain of 1.40 pounds per head. Bermuda grass and lespedeza produced an average daily gain of 1.02 pounds per head, and kudzu was the only type of pasture at Tifton on which the daily gains of the steers exceeded those of the woolly fingergrass pasture, the average for kudzu being 1.60 pounds. The introduction of woolly fingergrass has revived hopes of providing productive pasture on poor upland soils of the Cotton Belt. It is both palatable and nutritious but, unfortunately, has failed thus far to produce viable seed. Breeding designed to overcome this weakness was begun this year.

During the past year, three new lettuce varieties or strains have been released to the seed trade. One of these varieties released to seedsmen under the designation Columbia No. 1 is a crisp heading sort similar in appearance to the New York and is adapted to culture in the eastern part of the United States. It appears to be resistant to tipburn and better adapted to eastern conditions than any strain of the New York type of lettuce previously grown. Another variety is a midseason or summer crop, one adapted to the Salinas-Watsonville section in California and designated as Imperial 847. It appears to be brown blight-resistant. The third variety of the group is a mildew-resistant strain of the Grand Rapids variety for greenhouse culture. It has been released under the name Grand Rapids No. 1.

Fertilizer Placement

In cooperative tests having to do with the placement of fertilizer in the soil with reference to the position of the tobacco plant, striking results were obtained with respect to both the survival of transplants and the final growth and quality of the crop. Perhaps the most critical period in growing the tobacco crop is that immediately following transplanting, a good stand and a quick, even start in growth being highly important. Certain placements of the fertilizer resulted in a high mortality of plants, so that although the crop was replanted two to four times perfect stands were never obtained and the growth of the surviving plants was irregular. Side placements have produced uniformly good results, whereas mixing the fertilizer in the band of soil from 4 to 6 inches in width and depth around the plant gave poor results. When the fertilizer was placed in a band underneath the plant, the results were unsatisfactory. Where the fertilizer was drilled in the open furrow and stirred with the soil and the row then ridged, the results as a rule were good, although they did not equal those obtained with the side placements. Split applications of fertilizer, with a portion applied to the side, usually produced the highest yield and value of crop obtained in the tests. In comparative tests with standard-strength and high-analysis mixtures, the results obtained were in close agreement.

On some of the principal cotton-producing soils of the Southeast the reinforcing of fertilizers with magnesium and calcium neutralizing agents has rendered fertilizers more effective in the growing of cotton. When fertilizers are made nonacid-forming, the less costly soluble organic and inorganic sources of nitrogen may be as efficient on many cotton soils as the more expensive natural insoluble

organic sources of nitrogen and all the fertilizer may be applied at or in advance of planting on many soils without serious danger of loss by leaching. The application of such fertilizers at planting tends to reduce the production cost of cotton when compared with the system of applying the mixture containing part of the nitrogen at planting and the remainder as a separate application after the crop is up. Fundamental work with machine placements of fertilizers to cotton, in cooperation with the Bureau of Agricultural Engineering, has shown side placements to be the most satisfactory. Efforts are being directed toward devising practical and inexpensive means of accomplishing this placement of fertilizer.

WILDLIFE

WITH allotments from emergency funds aggregating $8,500,000, the Bureau of Biological Survey on July 1, 1934, undertook the task of averting the most serious crisis with which waterfowl in this country have ever been faced. Of this amount, $8,100,000 has been expended, and the balance has reverted to the Treasury.

The most protracted drought in our history, drainage operations, and attempts to reclaim land for agricultural purposes had combined to bring about an extremely serious shortage of waterfowl breeding, resting, feeding, and wintering grounds. This condition, augmented by an increase in botulism and other waterfowl diseases, large-scale hunting activities, and the toll taken by predatory animals had so alarmingly reduced the waterfowl population as to forecast extinction of many species within the space of the next 5 years unless preventive steps were taken at once.

To save waterfowl and restore them to approximately their former abundance was and is the primary consideration of the Survey's activities, but it should not be overlooked that these activities constitute a powerful weapon in the battle toward economic recovery and reconstruction. This will be evident from consideration of the following integral parts of the duck-restoration program:

1. Purchasing large areas of submarginal land, which in practically every case has proved entirely unfit for agricultural usages. The sale of their land has enabled distressed farmers to move to more desirable locations and start anew.

2. Employment by the Survey of a large number of men, many of whom were on relief rolls. This is especially important, since, in the main, these activities are located in drought-stricken areas that have been the hardest hit by the depression.

3. The construction of storage dams, marsh embankments, and other water-impoundment devices in the course of the development of practically every wildlife refuge. These improvements will conserve valuable water resources which are now being dissipated to an alarming degree. The drought has emphasized the need for the conservation of water, and the popularity of the Survey's activities in the Dakotas, for example, shows that there is great public interest in this phase of conservation.

4. The propagation and protection of heavy growths of vegetation for waterfowl food and cover. Such work forms an important part

of the refuge-development program and helps to repair the damage which the uncontrolled action of wind and water has inflicted.

Between $800,000.000 and $1,000,000,000 is spent annually for sportsmen's equipment and outdoor facilities, and a million people depend wholly or in part upon some aspect of this business for their livelihood. In addition, there is the fur industry, with an estimated $500,000,000 annual turn-over in retail trade. The threat to industries of such proportions obviously merits attention.

The educational and esthetic value of wildlife is important, and laboratory facilities are being provided on a number of the waterfowl refuges. The fund of data in the natural sciences will thus be enriched. The hunting, as well as the observation, of waterfowl furnishes millions with healthful recreation. On many wildlife refuges the Survey is developing picnic grounds and bathing facilities for the use of the public.

The total acreage of bird-refuge land actually administered by the Biological Survey as of February 29, 1936, exclusive of the acreage of those refuges located in Alaska, Hawaii, and Puerto Rico, and exclusive also of a large acreage of big-game land on which birds are also protected, is 2,118,433 acres and includes more than 100 refuges. There are additional areas on which options for purchase have been approved by the Migratory Bird Conservation Commission. These areas total some 999,398 acres and include 36 areas that are now, or soon will be, functioning as waterfowl refuges through special permits from the owners. Thus it may be said that there are now under the Bureau's jurisdiction over 3,000,000 acres of bird-refuge land.

Big-Game Refuges

Two outstanding big-game refuge projects have been inaugurated under the $6,000,000 appropriation approved June 15, 1935. One of these provides for the enlargement of the Elk Refuge in Teton County, near Jackson, Wyo., to take care of the great bulk of the elk of the southern Yellowstone herd which winter in the Jackson Hole country. This project involves the acquisition of 20,000 acres to be administered in connection with the 4,500 acres already owned and operated at that point. Roughly, the area includes the land lying north of Jackson, east of the Jackson-Moran Highway, south of the Gros Ventre River, and west of the boundaries of the Teton National Forest. The elimination of private interests from this area and the restoration of grazing therein will provide an abundance of winter feed for the elk. This project is very important.

The other project is known as the Hart Mountain Antelope Range, in Lake County, southeastern Oregon. It has been established by Executive order in connection with the organization of grazing districts under the Taylor Act. The purchase of some 25,000 acres of privately owned lands has been initiated under the 1935 appropriation above mentioned.

Other pending projects for the designation of ancestral game ranges have been agreed upon in connection with the grazing districts being organized under the Taylor Act.

Improvement of big-game refuges by C. C. C. camps has continued at the National Bison Range, Mont.; the Niobrara Game Preserve,

Nebr.; the Charles Sheldon Antelope Refuge, Nev.; and the Wichita Mountains Wildlife Refuge, Okla.

Federal authority over migratory birds will be reinforced and extended by an act of Congress approved June 20 to give effect to the convention between the United States and Mexico for the protection of migratory birds and game mammals. The United States Senate on April 30 consented to the ratification of the treaty. Mexico has not yet ratified the treaty. It will take effect on the exchange of ratifications. Federal authority over migratory birds has heretofore depended on the Migratory Bird Treaty with Great Britain. The new treaty reinforces this authority by providing for a dual basis for the Federal regulations conserving ducks, geese, and other migrants.

With the signing of an agreement by State agencies in Ohio, nine States are now cooperating with the Biological Survey in investigations to learn how to increase, maintain, and use wildlife resources and to show on trial areas how research results can be applied. The cooperating States are Alabama, Connecticut, Iowa, Maine, Ohio, Oregon, Texas, Utah, and Virginia. These were selected for research on a regional basis and to avoid duplication of effort. Each State program is arranged so that the information obtained may be applied in a large area.

AGRICULTURAL ENGINEERING

The best regulation and use of the waters of at least 11 of the Western States depend upon reliable forecasts of stream flow. Advance knowledge of stream flow is indispensable to the proper operation of irrigation, hydroelectric, and flood-protection works. In the making of such forecasts, however, adequate snow surveys are necessary, and snow surveying has not yet reached the required proportions. Accordingly, the Bureau of Agricultural Engineering, in cooperation with other Federal and State agencies, is planning several hundred new snow courses for survey during the winter of 1936–37. This undertaking will extend the snow-survey work into areas not now served.

This Bureau has had the responsibility of coordinating, standardizing, and extending the snow-survey work of various agencies. It issued forecasts of the 1936 season's water supply for the greater parts of California, Oregon, Nevada, Idaho, Utah, Wyoming, and Colorado shortly after April 1936. These forecasts indicated that most of the streams would yield 100 to 125 percent of the normal supply and that the run-off would equal the highest recorded in the last 10 years. With this assurance, irrigators prepared to plant all the area that had heretofore been irrigated.

However, the unusually warm spring resulted in a very early and very heavy run-off. In areas having inadequate storage facilities much water ran to waste; and in some areas little irrigation water was left for late-season needs. Warned against planting late crops, farmers adjusted their cropping programs and avoided certain loss. Where long snow-survey records were available, it was possible to distribute the water among the storage reservoirs in such manner as to effect the greatest economy in its utilization.

The net safe yield of water for irrigation from western watersheds depends upon reservoir storage. Evaporation from lakes and reservoirs results, however, in a material loss. This loss is largely unavoidable, but knowledge of its magnitude and of the factors that influence evaporation helps in devising means for reducing the loss, in estimating the available reservoir supply, and in determining the feasibility of reservoir-construction projects. It is useful also in planning irrigation, municipal water supply, and hydroelectric projects. The data collected by the Bureau provide the basis for estimating the evaporation losses from the surfaces of stored water and from water transported long distances in open conduits.

The best use of water requires an understanding of soil characteristics, particularly those related to the absorption and retention of water. Studies of the rate of movement of capillary moisture have high practical value in determining soil-moisture conditions, with or without irrigation. Studies of the infiltration of water into the soil indicate what types of soils can best be irrigated, and how land should be prepared for irrigation. Research in the Bureau of Agricultural Engineering is throwing new light on these problems.

Irrigation to protect high-value crops against drought is receiving increased attention in the Eastern States. Where sufficient water can be had at reasonable cost, the practice is profitable in growing fruits and vegetables. In the spring of 1936 irrigated strawberries on the Eastern Shore in Maryland produced an excellent crop of high-grade berries. The increased income this year practically paid the cost of installing the irrigation equipment. Adjacent unirrigated fields, because of drought, produced no marketable berries. Profitable results from irrigating fruits and vegetables were reported also from Florida, Michigan, New Jersey, Ohio, Virginia, and West Virginia. But results from the irrigation of general field crops in the East do not as a rule justify the expense.

Common tillage practices in the production of cotton can readily be modified so as to increase the yield and lower the cost of production on at least one soil type—Greenville sandy loam. This has been discovered in tillage experiments carried on for 5 years at Prattville, Ala. The methods and the tools used in tillage influence both fiber length and yield. Operations repeated each year with implements that improve or injure the soil structure have a cumulative effect on the crop. The depth and the method of turning under green manure crops also influence the yield of cotton on this soil.

Improved Farm Equipment

New or improved equipment is being put out by farm-machinery manufacturers partly as a result of investigations by Department engineers. This machinery includes (1) fertilizer distributors that place the fertilizer, during the planting operation, at the proper distance to the side and below the seed to be of greatest benefit to the crop; (2) the variable-depth cotton planter, which eliminates the necessity for replanting except under extraordinarily unfavorable weather conditions; and (3) a basin-forming attachment for the lister when used in planting corn, designed to form dams at short

intervals in the lister furrows to conserve moisture by holding rainfall and to prevent or reduce erosion by water and by wind.

Farm-machinery sales have increased. Information received by the Bureau of Agricultural Engineering indicates that the value of all the equipment sold in the United States by manufacturers in 1935 was $325,566,909, as compared with $248,979,523 in 1931. Sales during 1936 will probably exceed $400,000,000. Much of the increase will be due to the sale of newer types of equipment, such as the general-purpose tractor on pneumatic tires, and the small combined harvester-thresher. It is estimated that no fewer than 7,500 combines operated from the tractor by power take-off and mounted on pneumatic tires were used this year in the Corn Belt and the Southern States. These machines harvest a variety of crops satisfactorily, particularly soybeans and small grain. The power take-off, which of course does away with the need for an engine on the combine, reduces the cost of the machine greatly; and the pneumatic tires make lighter construction possible. Though the small machines have a narrower cut than the machines formerly in common use, the rate of harvesting is not proportionately lower, because the smaller machines can be pulled at higher speeds.

Tests conducted at the Department's cotton-ginning laboratory at Stoneville, Miss., have attracted wide interest. Many ginners are modernizing their gins and following the recommended methods. In the 1935–36 ginning season 200 seed-cotton driers, built on a principle patented by Department engineers, conditioned about one-third of a million bales of damp cotton for ginning. About 300 such driers may be in operation in the 1936–37 ginning season.

In buildings for the storage of fruits and vegetables in commercial quantities, especially in cold climates, the control of temperature and humidity (or air-conditioning) is important not only for the safe and economical holding of the crop but for the prevention of damage to the buildings. Investigations of potato storage by this Department in cooperation with the Maine Agricultural Experiment Station have developed an improved method of obtaining the desired air conditions. These methods take advantage of the well-known fact that moist air coming in contact with a cold surface deposits moisture, and in so doing liberates about 1,000 British thermal units of heat per pound of moisture condensed. In this way the walls of the storage house are dampproofed and the ceiling is insulated more than the walls, so that high humidities to aid in keeping the potatoes in good condition can be held without damage to the building. In cold weather excess moisture given off by the potatoes is drained away as water, with much less loss of heat from the building than if it were carried away as vapor by ventilation. Heating and ventilation during cold weather are reduced to the minimum and loss of weight by the potatoes is lessened. The same principle is applicable to the storage of other vegetables and fruits. With some modification it may be useful in buildings for livestock and for other purposes.

Improvement of Farm Homes

The improvement of farm homes remains one of the unaccomplished tasks of agriculture. Observations in many parts of the country indi-

cate that comparatively few farm families have as yet found it practicable to provide themselves with modern homes either through new construction or by modernizing the old dwellings. Sooner or later there must be a tremendous volume of farm-home improvement and new construction. Therefore this Department, in cooperation with the State Universities of Wisconsin and Georgia, is gathering facts about the comfort and service provided by various types of farmhouses found in the North and in the South. One phase of the investigation deals especially with the factors in house design that contribute to comfort in hot weather. The results should aid materially in the development of improved designs.

GRADING AND STANDARDIZATION

A NEW principle entered the grading and standardization work of the Department this year. It was the use of the referendum to decide whether or not a group should have mandatory inspection based on Federal standards for market quality and condition.

This new development was provided for in the Tobacco Inspection Act, signed in August 1935. Permissive inspection, which began in 1929, has demonstrated the feasibility and practical value of tobacco inspection based on standard grades. Several referenda indicated that tobacco growers in large numbers want mandatory inspection. They see in it a means of reducing the costs and improving the efficiency of marketing and distribution.

The tobacco-inspection service has for its object the certification of the grade on each lot of tobacco offered for sale at auction. It is designed to overcome the average producer's lack of technical knowledge of the qualities and values of his tobacco and to improve the general technique of marketing the crop. It is coupled with a price-reporting service that gives the current average prices for the various grades. These two services enable the grower to have, at the time he sells his tobacco, a competent and disinterested judgment on the quality and approximate market value of his offering.

As a result of favorable votes in several referenda, mandatory inspection service has been ordered for 18 tobacco markets, and another market has voted favorably on the matter and will soon be designated. The law, however, has been challenged in the courts, and a temporary injunction issued, which for the time being stops the grading of tobacco on three designated markets in South Carolina.

The first official inspection service known to have been provided for any agricultural commodity was a tobacco-inspection service. It was passed by the Virginia House of Burgesses in 1619. Since then much legislation pertaining to tobacco inspection and to other phases of production and commerce in tobacco has been enacted. However, the Tobacco-Inspection Act is the first piece of national legislation providing for tobacco inspection that has had for its primary object the protection of the producer's rights and interests when he offers his tobacco for sale. The first State legislation of a similar character was enacted by Virginia in 1933. It related to fire-cured tobacco, type 21, which is produced in a group of counties south of the James River.

An educational program has been started in connection with the mandatory tobacco inspection and the market-news service to promote improved methods of sorting tobacco and preparing it for market. This program is limited at present, but it has met with an encouraging response from county agents, agricultural teachers, farmers, and the tobacco trade.

Permissive Federal Standards

There has been for many years an extensive use of Federal standards on a purely permissive basis. Along with the use of mandatory Federal standards for cotton and grain under certain interstate marketing conditions, the voluntary use of optional Federal standards has developed. Progress has been particularly noteworthy in the fruit and vegetable industry. Ten years ago the Federal Inspection Service inspected 198,075 cars. Last year it inspected 395,250 cars. In the concurrent development of the two methods the compulsory and voluntary use of Federal standards have promoted each other. This year marks the first meeting of compulsory and voluntary action in the case of a single commodity.

Extensively revised standards were recently promulgated for grain and cotton to meet the needs of changing production and marketing practices and to embody new knowledge.

The United States standards for cotton also serve as the universal standards for American cotton. Accordingly representatives of nine principal European organizations were consulted in the revision of the standards. Leading representatives of American organizations of producers, manufacturers, and shippers were consulted also. The revised standards became effective in August 1936. They are more representative than the former standards of the characteristics of the cotton now produced and are more readily used. The number of grades is reduced from 37 to 32, and the number of standard boxes from 25 to 13.

Along with the whole question of what constitutes quality in cotton, methods are being studied for the further measurement of quality. New techniques are being devised and tested. They may permit further improvement in the standards.

The revised grain standards were drawn to meet changes in merchandizing, milling, other processing, and baking. All groups interested in grain marketing from the farm to the export wharf were urged to examine and test the revised standards before they were promulgated. Somewhat less significant, but not less useful, revisions are being made in the permissive standards from time to time.

Farm products inevitably include wide ranges in quality. Standards must change with significant changes in production practices. Sometimes preferences and requirements of consumers vary decidedly in different markets. Changes in industrial technique or in methods of marketing may change the importance of certain quality factors or quality standards. New knowledge of nutritive values may upset previously formulated specifications of desirability, and new techniques for the measurements of quality may make improvements possible. It is, therefore, necessary to revise the standards periodically.

Improvements in Standardization

The first Federal standards were largely empirical, but in expert hands they served. As a basis for transactions between distant points, for a common trade language between farmers, dealers, and consumers, for market quotations, for price and market comparisons, and for agricultural financing and credit, they answered many vital wants. But research and experimentation in the Department steadily improved the standards and the methods of applying them. Methods, instruments, and other apparatus were adapted to specific ends. Many public-service patents have been obtained for apparatus designed especially for grain standardization and inspection, and for other agricultural commodities. This year saw the conclusion of an exhaustive practical test of a new grain-sieving device known as the Federal dockage tester, the making of new conversion charts for use with electric meters in determining the moisture content of Argentine flint corn and several other grains, and an improved refractometric method for determining the oil content of flaxseed. This method requires only a half hour instead of the 16 to 24 hours formerly required. In commodity grading much still remains subject to human judgment and skill, particularly in regard to such factors as flavor, body, and color in butter. But accurate measurements, through mechanical or chemical means, are steadily replacing the earlier empirical knowledge and ways.

These techniques are the results of laboratory and economic research supplemented by practical observation. The studies are frequently intricate but the resulting tests must be simple and practical. As a general rule, the standards reflect the normal spreads in the market value of a commodity. The steps between grades correlate fairly closely with the price differentials that prevail in the market. Research is providing more precise measures of the price significance of separate quality factors. Some quality factors that affect prices, however, may not yield to statistical measurements, and it is necessary then to rely on observation and judgment.

The relationship between the grades and market price differentials does not remain constant necessarily. Price spreads between grades of a product frequently reflect the proportions of the product that fall within each of the grades. There are other influences. Buyers' opinions as to value do not always correspond to intrinsic value. Before the Federal standards were adopted, for instance, "pea-green color" was the quality factor in alfalfa hay that commanded a premium. Research disclosed that the feed value of alfalfa hay correlates more closely with its leafiness. Then the factor of leafiness was given greater emphasis in the standards. Steadily increasing premiums paid for leafy as compared with pea-green alfalfa apparently reflect the influence of the revised standards. Present studies give special consideration to the carotene or provitamin content of hay.

Naturally, standards have limitations. They cannot meet all requirements. Some believe they are too general, and do not adequately measure variations in quality. This difficulty often lies in the products. As research yields more accurate measures of quality factors, the descriptive standards will become more precise.

Sometimes the margin recognized between the upper and lower limits of some grades may seem to be too wide and may not adequately reflect qualities peculiar to the products of various regions. But the national grades have to serve the national industry. It is impracticable to narrow them so as to cover all gradations in quality. Regional characteristics that have market value may be covered in additional local notations. It may prove desirable for some commodities to have different sets of standards for different stages in marketing. Special consumer grades may sometimes be practicable for retail use.

Consumer Interest Awakened

In fact, an outstanding recent development has been the awakening of consumer interest in commodity standardization. Led by informed and organized groups, the consumers' voice increasingly demands grade specifications that can be used in making household purchases, and truthful and informative labeling based on these grades. Consumers have a right to know what they are buying. The Federal standards for meat are adapted to consumer needs, and the Federal labeling of meats by grade has had excellent consumer response. Beginning in 1927, in the first full year of this service, 28,000,000 pounds of meat were officially graded and stamped. During the last fiscal year 423,000,000 pounds were so graded and stamped. Originally only beef was stamped; now beef, lamb, mutton, sausage, and certain other meat products are included. Seattle in 1934 passed an ordinance requiring that all beef, lamb, and mutton sold within the city limits be graded and stamped. Schenectady, N. Y., has passed a similar ordinance.

The labeling of canned fruits and vegetables according to grade has made rapid progress. The movement has strong consumer support, and strong support among certain groups in the canning trade. One large chain-store organization is using Federal grade designations on its pack of several fruits and vegetables and giving them national distribution. National advertisers, however, are reluctant to adopt uniform grade labeling. They fear that their brands will lose prestige. But brands do not give consumers the information they want. There is no reason, moreover, why both the brand name and the grade designation cannot be used on labels. The Federal standards for butter, eggs, and certain kinds of poultry are suitable for consumer use. Labels based on these grades are coming into retail use.

Possibly the next line of decisive progress will be in the greater use of Federal grades by consumers. That may require the development of special grade specifications or descriptions.

HOME ECONOMICS

Letters that pour into the Bureau of Home Economics indicate that the American public has turned "consumer conscious." Men as well as women are asking daily for help in planning budgets. They want to know how to get the most for their money, no matter how adequate or how limited their income. The economic situation of recent years has made families at all levels of living conscious of the need to budget their resources, to buy wisely, and to save. This

is true of heads of families and of single men and women whose letters indicate a good educational background, but it is equally true of those whose letters indicate that their educational opportunities have been meager. It is true of families who are trying to adjust to the budgeting of incomes of $5,000 to $6,000 a year when they formerly were distributing very much larger amounts for family needs, and also true of families who are trying to make ends meet when the total resources consist of less than $60 a month from work relief.

The solution of such problems must come in part through study of the spending habits of American families. Yet there has never been a comprehensive study of American consumption habits and needs. For this reason the Bureau of Home Economics is now cooperating in such a study, which has been launched under the Works Progress Administration.

When the Emergency Relief Appropriation Act of 1935 was passed proposals to undertake a study of consumption habits as a Federal Works project were submitted jointly by the National Resources Committee, the Bureau of Home Economics, and the Bureau of Labor Statistics, the latter Bureaus constituting the administrative agencies. The study of consumer purchases was approved by the Works Progress Administration in December 1935. Methods for collecting, editing, and tabulating the necessary data were developed cooperatively by the Bureau of Home Economics, the Bureau of Labor Statistics, the National Resources Committee, the Central Statistical Board, and the Works Progress Administration.

The work of selecting a staff and of setting up regional and local offices in 27 States was begun in a preliminary way in January 1936. The field work, begun shortly thereafter, is now nearing completion, and statistical pools are engaged in tabulating the data. Information has been collected from about 50,000 families interested in cooperating to the extent of giving facts about their income, about the age and occupation of their members, and about the commodities and services they buy. About half of these families have given more detailed information on their expenditures for housing, food, clothing, transportation, medical care, and various other types of goods and services, and on their savings. In addition, from a smaller number of families, detailed information has been obtained on the kinds and quantities of food, household equipment, furnishings, and clothing procured.

Families living on farms, in villages, and in small city areas are cooperating with the Bureau of Home Economics. City families are cooperating with the Bureau of Labor Statistics. When all of the facts are consolidated we shall know for the first time what typical American families actually buy and what kind of living they get.

The cooperating families represent different occupations and family incomes ranging from $250 up to $5,000 or more a year. The facts will typify living conditions in different sections and will show variations due to rural and city living.

Not only will the families profit who assist in the study but the findings will be valuable to all families who want guidance in budgeting. Consumers' wants should eventually be met more satisfactorily because the information, when summarized and interpreted,

will help farmers and manufacturers to produce with less waste. Merchants will have a better guide to probable changes in consumer demand. The United States Chamber of Commerce requested such a guide a few years ago.

The social value of the study will be important. The public, and local, State, and Federal agencies concerned with public health and general welfare, will have new facts to show the prevailing levels of living in this country and to indicate the need for betterment.

Value of Diet Statistics

Facts about what the public eats are indispensable in planning farm production and distribution. Such facts also have an important bearing on education in dietary problems. The general well-being of a people is largely dependent on the adequacy of their diet. Many families who now fail to get a satisfactory diet can have a satisfactory diet for the same expenditure if they will consider both nutritive value and cost in choosing their foods. In order to help them the Bureau of Home Economics prepared Farmers' Bulletin 1757, Diets to Fit the Family Income. This bulletin discusses scientific principles of nutrition and food economics in nontechnical language.

During the past year, the Bureau analyzed the kinds and quantities of food purchased and the nutritive value of the diets of wage-earning families. The necessary records were collected by the Bureau of Labor Statistics, in conjunction with a study of the disbursements of families of wage earners and low-salaried clerical workers. About 2,500 records became available for this analysis. As a result, extensive figures will soon be available on the kinds and quantities of food purchased by city wage-earner families in different sections of the country at different seasons of the year, and at different levels of expenditure.

The diets have been analyzed for their nutritive content and appraised in the light of dietary standards. A preliminary report of the work appeared in the July 1936 issue of the Monthly Labor Review. This report, with an analysis of the diets of nonfarm American families as shown by studies made during the last 20 years, was sent to the International Labour Office and to the health committee of the League of Nations in December 1935.

The quantity of all food purchased (on a per-capita basis) increases, as one would expect, with the expenditure for food. This was shown by classifying into groups the diets of all families studied, by $32 intervals adjusted to 1935 price levels. From a level of expense for food of $32 to $65 per capita per year to a level of expense for food of $258 to $290 per capita per year, the increase in weight of food per capita as shown by this classification was almost threefold. Naturally, however, the percentage increase from one level to another was much greater at the lower than at the upper levels of expenditure.

For some food groups, such as the grain products, purchases increase relatively little as expenditures increase. Foods from the cereal grains usually are cheap in relation to their ability to assuage hunger. Hence, they appear, as might be expected, in generous amounts in low-cost diets. as well as in expensive diets. The con-

sumption of milk increases rapidly with increasing expenditures at the lower levels, but less rapidly after the pint-a-day level of consumption is reached.

With increasing expenditure for food, changes in the quantities consumed of fruits and vegetables (other than potatoes and dried legumes) are very striking. The increase from the lowest to the highest level of expenditure is almost sixfold. Citrus fruits, tomatoes, and leafy, green, and yellow vegetables comprise about 40 percent of the total in each level of expenditure for food. These fruits and vegetables are mentioned especially because of their significance as sources of vitamins and minerals.

The increase in the consumption of lean meats and fish is almost threefold between the lowest and highest levels of expenditure, while the consumption of fatty foods almost doubles. Butter consumption increases almost five times, but the consumption of other fatty foods remains almost constant. Butter seems to be used in addition to and not as a substitute for lard, bacon, salt pork, and other fats and oils.

The fourth of the nonfarm population that spends the most for food consumes about one-third of the milk, fruits, vegetables (other than potatoes and dried legumes), meat, fish, and eggs, whereas the fourth that spends the least for food consumes about one-sixth of those products. Differences in consumption at different economic levels in any one region are much more important than differences between geographical regions at any one level.

Social Implications of the Data

The most frequent level of expenditure for food among the families from whom dietary records have been taken was found to be that ranging from $100 to $130 per capita per year (1935 price levels). About half of the families were spending less than $130 per capita per year. According to 1935 prices, a minimum-cost adequate diet could be obtained with careful food selections for just about $130 per capita per year. The inference is that the diet of half the nonfarm population probably fails to provide a desirable margin of safety over minimum requirements. At the lowest levels of expenditure for food the calorie intake is far below the average for the population and far below the probable need; one need not, therefore, be surprised to find retarded growth in children and undernutrition in adults.

On the other hand, the figures shown for families spending the larger amounts for food probably represent quantities available to the household rather than quantities actually eaten. They include considerable household waste. Hence the quality of the diets of the higher-income groups depends on how much and what is wasted. Calorie for calorie, the food supply purchased by families spending the largest amounts for food is only slightly higher in proteins, minerals, and vitamins than the diets of low-income groups. But if the milk and vegetables and fruits purchased are almost completely consumed, while waste occurs principally in the fats, sugars, and grain products, the food actually eaten by the higher-income groups may be considerably richer in minerals and vitamins than the diets of low-income groups.

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The percentage of the calories purchased in the form of grain products is much higher in low-income groups than in the higher income groups; it ranges from more than 40 percent in the lowest level of food expense studied to somewhat less than 30 percent of the calories at the highest level. An opposite trend may be observed for most other groups of foods. The percentage of calories derived from milk almost doubles as the expenditures for food increases, and the percentage derived from lean meats, fish, and eggs increases significantly.

Futher study of these consumer purchases will furnish more authoritative figures on food-consumption habits and on food expenditures. It will show, for example, how food-consumption habits may vary among families spending the same amounts for food, but representing different socioeconomic groups. It will also provide figures on the proportion of the native-white families of each type that represent different levels of food expenditures.

There is widespread interest in these data, not only from the standpoint of science and social welfare but also from the standpoint of the economic implications. The governments of many nations, as well as international and national bodies of economists, educators, and others interested in social and economic planning, are giving much attention to these problems.

COMMODITY EXCHANGE ADMINISTRATION

To improve and protect the means furnished by properly conducted futures-contract markets for the hedging of price risks by growers, dealers, and processors of essential agricultural products, the Grain Futures Act of 1922 was strengthened by amendment on June 15, 1936. It was extended to cover cotton, rice, millfeeds, butter, eggs, and potatoes, and the short title changed to the Commodity Exchange Act.

The principal amendments include the following:

That commission merchants and brokers executing orders for customers in a contract market shall register with the Department of Agriculture and shall keep adequate accounts and records, which shall be available for official inspection; that copies of all bylaws, rules, and regulations adopted by contract markets shall be filed with the Secretary of Agriculture and their books and records be made available for inspection; that operators of warehouses from which any commodity is made deliverable on futures contracts shall keep such records, make such reports, and permit such visitation as the Secretary of Agriculture shall require; that when so directed by the Secretary, each contract market shall provide for a period, after trading for future delivery in any delivery month has ceased, in which to make settlement by delivery, such period to be not less than 3 or more than 10 business days; that each such market shall require the party making delivery to furnish the party receiving delivery written notice of the date of delivery at least 1 day prior thereto; that deliverable commodity grades must conform to United States standards, if such standards shall have been officially promulgated; that receipts of federally licensed warehouses, as such, shall not be discriminated against in deliveries upon futures contracts.

Provisions of importance to cooperatives are that no contract market shall forbid the payment of patronage dividends by a cooperative association to bona-fide members; that a properly qualified cooperative association shall not be excluded from membership in and trading privileges on a contract market unless such exclusion is authorized after notice and hearing before the Commodity Exchange Commission, except for failure to meet its obligations with the clearinghouse of the exchange; and that cooperative associations of the federated type are authorized to compensate on a commodity-unit basis their regional member associations for services rendered, provided such compensation is distributed as a dividend on capital stock or as a patronage dividend out of net earnings or surplus of the federated association.

Special protection has been thrown around the margin moneys of the customers of futures commission firms. The act requires all futures commission merchants to treat and deal with all margin moneys, including securities and property, as belonging to customers. Such funds must be separately accounted for and may not be commingled with the funds of the commission merchant or used to margin the trades or contracts or extend the credit of any person other than the one for whom the same are held.

The danger of excessive trading by individuals or allied groups is also given special attention. The Commodity Exchange Commission has wide discretion in fixing limits for speculative trading whenever it appears that such limits are necessary. Ample latitude for hedging is carefully preserved.

Fraudulent trading is made more hazardous. Criminal penalties may be imposed for various offenses, such as conducting a bucket shop, speculative trading in excess of a limit fixed for such transactions, the manipulation of prices, engaging as a futures commission merchant or floor broker without prior registration, trading against customers' orders, dealing in privileges, making wash sales and cross trades, and fictitious trading.

During the past year three cases pending under the Grain Futures Act of 1922 were dismissed following decision of the Circuit Court of Appeals of the Seventh Circuit that the law did not apply to past offenses. This defect in the original law has been remedied in the amended act, which provides penalties for any person who has violated the act as well as for any person who is violating the act.

COOPERATIVE EXTENSION WORK

The cooperative agricultural extension system operates in two principal fields of service: (1) It mobilizes Federal, State, and county facilities for helping farm people to solve their ordinary problems of production and marketing, homemaking, and country-life improvement. (2) In great national emergencies it tackles the resulting special problems. In the last few years it has taken an active part in the administration of production-adjustment programs: loans to farmers on stored crops; drought-relief measures; programs for the prevention of soil erosion; programs for debt adjustment and farm-credit improvement; and rural rehabilitation and relief.

In advancing these programs and activities the extension agents directly represented the Federal and State agencies. They acted as advisers and assistants in the organization and educational work, and functioned also in an administrative capacity in cooperation with local committeemen and producers' groups or associations. The county extension offices were the centers where committeemen and extension agents gave practical help and necessary instructions.

Local committeemen assisted capably in the administration of the national programs, particularly in dealing with regulations, rulings, agreements, papers, and essential forms. They relieved extension agents of much detail work and enabled them to handle more efficiently their larger responsibilities. In many counties local committeemen handled most of the local routine involved in the national programs.

Both paid agents and volunteer leaders furthered the educational features of the extension programs. Without the help of local volunteer leaders the rural boys' and girls' 4-H club work would have suffered. Local leaders helped also to conduct adult demonstrations and rural educational meetings. As a result farmers are coming to understand better how general economic conditions affect their individual problems. They discuss the effects of tariffs, quotas, price policies, price levels, currency measures, monetary systems, credit, taxation, and land-use policies. They are learning more about the interdependence of town and country and about the limitations of individual self-sufficiency. They are grasping the logic of group action in meeting emergencies. That agriculture is constantly changing and needs to make constant readjustments is now a potent conception in the rehabilitation of rural life.

The Extension Service aided farmers to take advantage of the agricultural conservation program inaugurated this year and to adopt other soil-improvement practices. It encouraged them to put land in better shape by seeding legumes for hay and for soil improvement, by sowing or treating pastures, by terracing, by planting cover crops, by strip farming, by listing, by building soil-saving dams. Such work is going forward on a scale never approached before.

When drought became serious this year the Extension Service aided farmers in growing emergency crops and in making the best use of the feed available. Temporary silos were built by the thousands. Feed-supply surveys were made and feed supplies budgeted. Exchange lists of feed were distributed. Feeds and emergency fodders were brought in from nondrought areas and distributed through central agencies.

Extension agents and local leaders cooperated with the regional agency set-up for clearing feed supplies. They helped farmers in pooling their orders so that they might obtain reduced freight rates. They helped farmers to make applications for crop-production loans and feed and seed loans. In cooperation with the Agricultural Adjustment Administration, the Extension Service conducted Statewide corn-fodder and feed-conservation campaigns. Water sources were tapped.

Combating Insect Plagues

Extension agents facilitated Federal and local cooperation in combating insect plagues. Thus in Illinois county agents were notified on June 8 that creosote would be made available by the Federal Government for building barriers against chinch bugs. At 9:30 the following morning orders for this Federal creosote were placed with the Federal purchasing agent. In all, 1,281,800 gallons were allotted to the 60 counties of the State where this pest threatened to do the most damage. About 10,000 miles of chinch-bug barrier were constructed in Illinois with the Federal creosote.

In areas affected by the drought, the consequences of which will be felt for years, the Extension Service is seeking with the aid of technical advisers to determine what the future farming program should be. It will encourage farmers to reorganize their cropping systems and to initiate different soil practices wherever the conditions of soil and climate warrant that course.

The farmers who have suffered are anxious for sound programs for both long- and short-time needs. They want the facts from which they may develop programs suited to their needs. The Extension Service recognizes the resulting responsibility. With recovery, and with time released from emergency projects, extension workers will not simply go back merely to old lines of work. New and larger problems demand attention, involving economic and social relationships as well as production factors. This calls for coordinated research and planning.

Accordingly, extension agents and research agencies are pushing a county agricultural planning project. After meetings with farm groups in every county it is hoped to develop recommendations for adjusting farm operations in terms of (1) national and international economic influences, (2) rational land use, and (3) farm management. Such recommendations should serve to develop county programs of the greatest significance.

City dwellers commonly think of farm life as synonymous with good food and health. Yet in some rural sections the problem of nutrition is acute. In certain areas some groups of farm people actually suffer from a lack of essential foods, though most of these foods could be produced there. The drought and the depression made this situation worse. Therefore the Extension Service gave more impetus to campaigns for growing and preserving food for home use, and the campaigns met with an extremely favorable response. County extension agents estimated in 1935 that the value of the food canned or preserved on farms in that year was $18,875,090. Home-produced vegetables, milk, eggs, meat, and fruit now appear on the table of many a farm where formerly the idea prevailed that the purpose of a farm was merely to produce crops for sale. The farmer who makes a living on the farm will have that living and some cash besides. When drought and depression strike, the family's living is surer and better.

The relief load was lightened, too, by the work done to produce food for home consumption in industrial centers. Thousands of gardens brightened mine settlements and industrial towns and helped to provide needed wholesome food. In one Eastern State the home-

garden and food-preservation movement required the services of about 125 garden supervisors and 175 canning supervisors. Four and a half million pounds of produce was grown in these gardens. More than a million cans of high-quality vegetables were prepared for distribution by welfare boards last winter.

Methods of Reducing Living Costs

Extension programs developed to aid people in lowering costs of living were popular. In fact, extension work with farm families was marked by constant adaptation to the problem of lowered family incomes, unemployment, relief, and social welfare. Encouragement and instruction were given in producing handicraft articles and other things for sale. Making, remodeling, and repairing garments were taught.

Drought and depression and recovery have forced farm people generally to recognize the needs of a profoundly changing country life. They will continue to want help and direction in adjusting themselves to these changes. By study and planning, many things may be averted or their bad effects modified. By planning and acting in cooperation with the community, the State, and the Nation, farmers may make recovery more lasting. It is the task of the Extension Service to furnish the information and the organizational help necessary to accomplish this result.

COOPERATIVE RESEARCH PROJECTS

Federal and State agencies cooperated in new and extended lines of agricultural research during the year, and improved their organization for greater service to agriculture and the general public. As usual the State agricultural experiment stations worked closely with other State agencies, with local organized groups, with each other in regional groups, and with this Department individually and in regional and national groups in efforts to plan and coordinate research. Cooperative research thus fostered dealt not only with the adjustment and relief policies of the National and the State Governments, but with permanent policies of agricultural production, land use, and rural life. The Office of Experiment Stations examined and recorded 818 new or revised formal cooperative agreements between bureaus of this Department and the experiment stations. The agreements covered 731 major research undertakings. All the State experiment stations and all but one of the Department's research bureaus participated. There were also many informal cooperative agreements, some of them of major importance.

Certain regional and national cooperative research undertakings which had been started on an emergency basis as parts of the national recovery program in 1934 and 1935 were modified and expanded to meet more permanent requirements. These studies brought more closely together the parallel interests of plant- and soil-science research and those of crop- and animal-production research with more thorough consideration of their economic and social influences. Studies of adjustments in farming by regions and type-of-farming areas from the standpoint of national agricultural adjustment received considerable attention in this connection and were

typical of the renewed and expanded efforts in cooperative research. In this case, a review of similar work done the previous year indicated the need for more complete studies.

A general plan for further action was agreed upon by State and Federal representatives at the meeting of the Association of Land-Grant Colleges and Universities in the fall of 1935, and formed the basis of widely extended cooperative research in regional adjustment policies in 1936. Nearly all of the States cooperated in this important study. This Department contributed to the work primarily through the Bureau of Agricultural Economics, but also through the Agricultural Adjustment Administration, the Soil Conservation Service, and the Forest Service. Among the State experiment stations it was common to find from 5 to 10 subject-matter departments actively engaged in coordinating their studies so as to fit both State needs and the national adjustment study program.

Another significant development in cooperative research during the year was the adoption of a policy for establishing and operating regional research laboratories under the Bankhead-Jones Act of June 29, 1935. Following negotiations with the land-grant colleges and the State experiment stations this Department issued a statement of policy on December 19, 1935, which embodied suggestions from its bureaus and recommendations from the State stations approved by the executive body of the Association of Land-Grant Colleges and Universities. Among other things, the statement of policy provided, as a basis for the activities of the regional laboratories, that the Secretary of Agriculture will receive suggestions from the experiment station directors and from bureau chiefs in this Department; that he will locate such laboratories solely with regard to the technical requirements and the facilities available; and that the Department and the State experiment stations will enter into memoranda of understanding regarding the work to be done, the cost of doing it, the sources of the funds, and the coordination of the laboratory research with regular activities of the States and the Department. Federal and State specialists will cooperate in preparing detailed plans.

Three Regional Laboratories Approved

In accordance with this policy three regional laboratories were approved during the last fiscal year; one for research in vegetable breeding; one for soybean research, with particular reference to the industrial uses of soybeans; and one for the study of grass breeding and pasture improvement. In the agreement covering the soybean laboratory, which is typical, 2 bureaus of this Department and 12 State experiment stations participated. It provides for integration of research at the laboratory with research at the experiment stations in the region and for the revision and reformulation annually of the research program.

The study during the year of grain storage on the farm is typical of the cooperative research into broadly important regional or national problems, initiated under the provision in the Bankhead-Jones Act for research by this Department other than at regional laboratories. In this undertaking, three of the Department's bureaus and seven of the State experiment stations, together with several other organized

Sate groups, cooperated in a manner which brought to bear on the problem the correlated knowledge and training of several different specialists. Besides avoiding duplication of effort, the arrangement avoided unnecessary duplication of research equipment.

Before the fiscal year ended, officials of this Department and a majority of the directors of the State experiment stations adopted a memorandum of understanding covering research relationships between the Soil Conservation Service and the stations. It recognized that effective cooperation in research by these agencies is primarily dependent on working to a common end, rather than on financing, and that each agency should contribute what it can in experience, knowledge, and personnel. It was agreed that such research as may be mutually agreed on with reference to soil erosion and its prevention requires mutual helpfulness, if it is to be fully effective. Accordingly, the memorandum provided that details of cooperative research projects within a State shall be planned and executed jointly by the State experiment station and the Soil Conservation Service. This understanding has far-reaching significance because it recognizes not only the need of regional policies in erosion control but also the limitation of action by individual States and Federal bureaus.

Federal and State agencies cooperated during the fiscal year in a national survey of plant and animal improvement. This provided the basis for material published in the Yearbook of Agriculture for 1936 regarding the character and availability of superior germ plasm in 19 plants and animals, and preliminary material for subsequent work on other animals and plants. This cooperative study brought together in a usable form the available information on animal and plant genetics and exercised a favorable influence on the further planning of similar studies.

As part of an enlarged Federal-State program in the study of land utilization, land-use adjustment, and soil conservation the inventory of soil resources was expanded to include 30 States. In six other States the work was completed. The widespread cooperative efforts in crop improvement were continued and expanded. Typical of these were the forage-crop investigations which were extended to include 11 States; the work in 5 States was completed. Other similar, widely cooperative researches were the breeding and improvement of grasses, corn, and potatoes.

Important New Cooperative Studies

Cooperative studies on other agricultural problems included several important new undertakings, among them a study of milk marketing in New England, the development of a program of agricultural economics in New England, studies of tobacco and cotton diseases, an evaluation of meat investigations, and a master study on human nutrition.

At a conference in November 1935, sponsored by the directors of the interested experiment stations, plant pathologists engaged in tobacco disease investigations in the southern tobacco-growing States formed a permanent organization known as the Tobacco Disease Council. This council laid plans for a coordinated attack on particular problems by special groups composed of experiment station and Department specialists and including representation from a privately endowed uni-

versity. A second conference, in June 1936, reviewed progress, took steps toward further voluntary coordination and cooperation along specific lines, extended the movement to more northern tobacco areas, and united it with the efforts of specialists on insect pests.

A similar conference, initiated by experiment station specialists with the cooperation of specialists of this Department on diseases of cotton, resulted likewise in the organization in February 1936 of a cotton disease council, with parallel objectives. As a result several serious disease problems of the Cotton Belt were taken up cooperatively by experiment station and Department specialists.

Food and nutrition specialists of several of the middle western experiment stations formulated a regional cooperative program of research on the nutritional status of college women. There is accumulating evidence of a relatively widespread chronic undernutrition among young women of college age. An executive committee has been appointed by experiment station directors to guide the work. The cooperation of the medical staffs of departments of hygiene and physiology has been enlisted.

FOOD AND DRUGS LAW ENFORCED

Artificially flavored and colored beverages which simulate genuine fruit products are frequently found to be in violation of the Federal Food and Drugs Act. Artificially colored, acidulated, and otherwise camouflaged products masquerading as bona-fide fruit beverages cannot fail to reduce the utilization and consumption of fruit. Operation of the Food and Drugs Act caused one manufacturer of an orange-oil-flavored beverage to change his formula to conform to the label, which indicated the presence of fruit juice. He began, in consequence, to purchase annually about 1,000,000 gallons of orange juice. This required some 10,000 tons of oranges. Previously the only orange product used in his beverage was orange oil.

In the spring of 1935 it became evident that maple sugar and sirup were occasionally contaminated heavily with lead. The contamination was traced to the use of sap buckets coated with lead alloy, and steps were taken to obviate this threat to health. But large stocks of the contaminated product were on hand. Investigations in this Department have suggested a simple procedure for the elimination of the poisonous contaminant. If this is successful, these stocks can be salvaged, and it will be unnecessary to divert thousands of gallons of the sirup and thousands of pounds of the sugar from food use, with consequent heavy loss to the producers.

One of the problems always before food and drugs law enforcement officials is that of the decomposition of foods. Procedures for the better preservation of perishable commodities and methods for the detection of unsound products, either in their raw state or as ingredients of food compounds, are very necessary. Research in the Food and Drug Administration constantly improves the technique. The application of various methods of analysis specially developed by the chemist, the bacteriologist, and the microscopist, to detect unwholesomeness in foods, not only results in the necessary condemnation and destruction of spoiled products, but frequently suggests better methods of handling and storage.

The study of vitamins has practical applications in food and drug enforcement. More than 4,500,000 gallons of cod-liver oil were used in this country last year, of which approximately 95 percent was imported. There are no statistics of the respective proportions used for human consumption and animal feeding, but it has been estimated that more than half of this oil is used for animal feeding, mostly for poultry. Cod-liver oil added to poultry feeds yields profits under efficient poultry management. When there is a lack of sunshine it supplies the necessary vitamin D to obtain maximum growth and egg production.

Surveys of the vitamin D content of the cod-liver oils used in poultry feeds revealed that a surprisingly large proportion fall below the required standard for vitamin D. Some of the oils are practically worthless. Examinations of a number of importations indicated that a significant portion of the imported oils are deficient in vitamin D. Cod-liver oils are now being examined for their vitamin content before their entry is permitted. The detention of shipments pending vitamin assays means inconvenience and expense to importers, but it is the only way to assure the users that the product is of satisfactory quality.

Livestock and Poultry Remedies

Of particular interest to farmers is enforcement of the Food and Drugs Act with respect to livestock and poultry remedies. Annually many of these are found to be worthless. During the past year the Federal courts in three contested cases upheld the Government's action against a contagious abortion remedy composed of cornstarch with a trace of potassium permanganate, which was sold for from $5 to $12 a pound; a protection powder labeled as a preventive for almost all the diseases of livestock and poultry, which consisted essentially of Glauber's salt and baking soda, sold at $7.50 per hundred pounds; a poultry remedy composed of water, alcohol, carbolic acid, and potassium chlorate, at 75 cents per quart, labeled an effective treatment for all poultry diseases.

Enforcement of the Food and Drugs Act on these veterinary preparations prevents serious losses to farmers. The price paid for the fake remedies is not the only thing involved. More serious is the fact that reliance on ineffective drugs delays the application of the proper treatment and sacrifices animals that might be saved.

ROAD CONSTRUCTION

Road construction administered by the Department during the year included work on the main through highways, the construction of secondary roads reaching into farming areas, extensions of the main system into and through municipalities, the improvement of roads in Federal areas, and the elimination of railroad-highway grade crossings.

A total of 27,373 miles of highways, roads, and trails, and 310 grade-crossing structures were brought to completion during the year. Of this mileage, 22,133 was improved with Federal funds administered solely by the Department. The remainder consisted of 204 miles of national-park roads built for the National Park Service by the Bureau of Public Roads; 2,319 miles of loan-and-grant projects of the Public Works Administration, also supervised by the Bureau of Public

Roads; and 2,718 miles in work-relief projects, the labor on which was supplied by the Federal Emergency Relief Administration. Other costs connected with these projects were paid with Public Works funds, and supervision was furnished by the Bureau of Public Roads and several State highway departments.

The major activity of the Department in road construction consisted of the administration of funds provided as direct grants to the States for relief of unemployment through highway and grade-crossing work and as Federal aid to the States for highway purposes. The work was carried on cooperatively with the various State highway departments in accordance with the general plan of administration of Federal aid for highways, but modified to meet the need of giving employment to those on relief rolls.

Work of this kind resulted in the completion during the year of 13,789 miles of roads and streets—7,355 miles on the Federal-aid highway system outside of cities, 755 miles on city extensions of the Federal-aid system, and 5,679 miles of secondary or feeder roads. On these classes of highways combined there were completed 310 railroad-highway grade-separation structures. Also completed were improvements on 22 miles of flood-damaged highways, on 236 miles of forest highways, and on 436 miles of highways through other public lands built by the Bureau of Public Roads, and 5,684 miles of forest roads and 1,965 miles of trails built by the Forest Service.

The current program at the end of the year involved a total of 25,812 miles in all classes of projects. It comprised 10,006 miles on the Federal-aid system outside of cities, 991 miles on city extensions of the system, 7,921 miles of secondary or feeder roads, 716 miles of forest highways, 261 miles of public-lands highways, 537 miles of national-park highways, 2,478 miles of loan-and-grant projects, and 2,902 miles of work-relief roads, the last three supervised by the Bureau of Public Roads as agent for other Federal departments. The current program also included 1,664 structures separating the grades between railroads and highways.

Railroad Grade Crossings

Authorization of $200,000,000 to eliminate danger at railroad-highway crossings under the Emergency Relief Appropriation Act of April 8, 1935, enabled the Department, for the first time, to participate in such work on a large scale with funds not subject to other demands for highway improvement. It has included in the program many urgently needed improvements not undertaken before because of hesitancy to spend large amounts of highway funds on a few structures. Approximately 2,000 crossings are to be eliminated with the new funds. Nearly 7,000 grade crossings have been eliminated with Federal assistance since 1916, but comparison with this figure does not give a fair picture of the value of the new work, because many of the new projects are of exceptional importance.

The work of the last year resulted in the elimination of 300 grade crossings either by structures or by relocation of the highway, the reconstruction of 10 existing structures, and the installation of protective devices at 185 additional crossings. Work under contract and approved at the end of the year will increase the number of grade

eliminations by 1,466 and the number of protected crossings by 813.

The total employment for the year on work supervised by the Bureau of Public Roads was 1,673,935 man-months, or the equivalent of an average full-time employment each month of 139,500 men. The number of individuals actually employed, some of them on a part-time basis, averaged approximately 195,000 persons per month. Indirect employment in the production and transportation of equipment and materials is estimated at one and six-tenths times the direct employment for work of the character done during the year. This resulted in an indirect employment of 2,678,000 man-months, and this, added to the direct employment, gives a full-time employment of 4,352,000 man-months, the equivalent of the full-time continuous employment of 362,000 men.

Secondary or Feeder Roads

Secondary or feeder roads have been receiving increasing attention from the Department. Actual participation in the construction of such roads began in 1933; 15,037 miles of secondary roads have been completed. Improvement of these roads is now a fixed policy of the Department. The general demand for better farm-service roads is reflected in the trend toward placing local roads under the control of State highway departments.

State and Federal highway officials must now plan for the improvement of secondary roads while they continue to make needed improvements on the main highways and to carry on work in still another new direction—the improvement of main routes through and around cities. Highway administrators face a difficult situation if they attempt to plan for these different classes of work on the basis of the incomplete knowledge now available. Serious mistakes and set-backs to highway development can be avoided only by knowing the amount of each class of improvement that is economically and socially justified and what will be the annual cost of needed improvements. Plans must be based on a thorough study of highway revenues, the sources from which they come, and the fairness with which taxes for highways are imposed.

Recognizing the need for highway planning on a businesslike basis, the Department has invited all of the State highway departments to participate in State-wide highway-planning surveys to be financed with 1½ percent of certain Federal highway funds and under specific legislative authority for the making of surveys and investigations for future work.

At the close of the fiscal year 40 States had indicated their desire to carry on planning surveys, and work was under way in 31 States. In these surveys data are being collected as to the highway mileage and its present condition of improvement, the extent to which each road is used, the extent to which various classes of residents use the different classes of roads, and the amount of taxes they pay for road purposes.

It is believed that the surveys will result in the assembly of facts necessary to the formulating of a definite, economically, and socially defensible, integrated highway-improvement program.

Henry A. Wallace,
Secretary of Agriculture.

1937 YEARBOOK OF AGRICULTURE

BETTER PLANTS AND ANIMALS

Book II

A SEQUEL TO THE 1936 YEARBOOK ON PLANT AND ANIMAL BREEDING

EDITORS

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IN SENDING *out to the public this second and last of the two yearbooks on genetics and breeding, I would not want anyone to think that they complete the account of the efforts of plant and animal breeders in the United States. On the contrary, I would wish these yearbooks to be looked on as pointing the way toward a field of activity that will accomplish much more in the future than has been accomplished in the past. Life is always changing because environment is always changing. There are always new types of diseases, new insect pests, changes in soil fertility, changes in consumer demands. The work of the plant and animal breeders is directed to meeting these changes. It has only just begun. We have reached our present stage of development largely by rule-of-thumb methods; but discoveries not dreamed of a few years ago are being made, and they counsel greater boldness in experiment and promise closer control because they give us an increased understanding of the processes that go on in the minute cells where life has its beginning.*

If genetics enables us to outdo nature's own efforts, it is because it is in the truest sense a science of cooperation with nature. We want to do different things than nature does—for example, in the creation of hogs with plump hams or wheat×grass hybrids with plump seeds—but we have to learn nature's methods of doing them. I think that more knowledge of how to cooperate with nature for our own good is the greatest need of the world today. Man's control of his own future may depend in the long run on whether his biological knowledge, which is constructive, can catch up with his knowledge of the physical sciences, which has taught him so much about how to destroy.

HENRY A. WALLACE.

WHAT THE BOOK IS ABOUT

GOVE HAMBIDGE, Principal Research Writer, Office of the Secretary

THIS book rounds out the work of the committee on genetics appointed by the Secretary of Agriculture in 1933. The task set for the members of the committee was to make a national and to some extent an international survey of practical breeding and genetic research with those plants and animals that are important in American farming. The first fruits of the work appeared in the 1936 Yearbook of Agriculture as a series of papers dealing chiefly with the major crop plants and classes of livestock. The present volume covers an enormous and varied field, dealing with garden vegetables, northern tree and bush fruits, subtropical fruits, flowers, nut trees, forest trees, forage grasses and legumes, Angora and milk goats, turkeys, ducks, fur-bearing animals, honeybees, and finally that good friend of the farmer, his dog.

Many of the articles are unique in that nothing of a similar kind has been done in their field, and the two yearbooks together probably contain the most complete and up-to-date account of breeding work and genetic research in relation to farm plants and animals that can be found gathered in one place. Even in those cases where there is little work of a really scientific nature to report—and this is true in some instances, for scientific breeding is by no means universally applied as yet—the writer of the article has explored possibilities and endeavored to foresee fruitful lines of effort. Indeed, the possibilities of the future are necessarily a theme that runs through both books, because this science of genetics is relatively young, and much as it has accomplished in creating new forms of life better suited to the needs of man than the old, its greatest achievements undoubtedly lie ahead.

The genetics yearbooks, it may be said frankly, have something of the hybrid nature of much of the material with which they deal. They are intended for two groups: (1) Readers who want to know what is going on in the field of plant and animal breeding in order to enlarge their understanding and to enable them to carry on their farming operations more intelligently, and (2) students and others who have, or expect to have, a closer concern with the science of genetics. The latter group comprises scores of thousands of individuals, including young people now in schools and colleges who will be the American farmers and the agricultural scientists of tomorrow—some of them future leaders in shaping agricultural progress; a large number of workers in various parts of the country who are engaged in the practical effort to create better plants and animals; and teachers, extension workers, and others whose business it is to know as much as possible about all the major factors in modern agriculture.

To combine the interests of these diverse groups in a single volume is a difficult task, but judging from the generous reception given the last Yearbook, the results have at least been characterized by a certain hybrid vigor.

Another purpose also underlies this survey of breeding and genetics. It is an attempt to make a frank appraisal of the present situation on a major segment of the agricultural front—not only to sum up achievements, but to expose weaknesses and shortcomings. The reader of the 1936 and 1937 Yearbooks will admit that the shortcomings have not been neglected. In almost every case, it is shown that we are far short of attaining the objectives that scientists believe we may attain with means as potent as genetics. As a matter of fact, though systematic breeding with such major crops as wheat has been going on for some time and has shown splendid results, it has only been begun in the last few years with many of the crops treated in the present book, and it has not had time to show what it can do. In other cases, the work is necessarily so slow that the results of the very earliest systematic efforts are only now beginning to be used. In the case of a new apple variety, for example, it takes nearly 40 years from the time the cross is made to the time when the variety is actually in commercial production. Tree breeders live in the present but think in the future.

On the positive side, however, there have been such outstanding achievements as the development of the wilt-resistant Marglobe tomato, which is now widely grown and saved the Florida producers from ruin; strains of cantaloups resistant to powdery mildew and of lettuce resistant to brown blight and powdery mildew—both of vital importance to California growers; snap beans resistant to some of the chief diseases that plague producers; cabbages resistant to yellows; sweet corn of such uniform and superior quality that it has remade canning practices; superior varieties of raspberries; blueberries far better than those produced by nature; a large number of improved navel oranges from bud selections; and many interesting new fruits created by hybridizing different kinds of citrus. Some of the new varieties and strains of plants developed by this constant activity are not yet quite ready for introduction.

Thus it is both heartening to discover how much has been accomplished and humbling to realize how little we know. There is probably not one writer of these articles who does not feel that the effort to sum up the past achievements and present status of the work in his field has been worth while. It has forced him to find out where we stand, to make a critical examination of what has been done, and to bring together many scattered fragments, so that their significance can be seen in the whole picture, including their relationship to the work of others in different fields. It would be well if a similar audit or stock taking could be made in other major branches of agricultural science, and, in fact, such a plan is now projected in the Department.

Much of the material was collected, as in 1936, through cooperative survey forms, or questionnaires, designed to survey the breeding and research work in all State agricultural experiment stations and in similar public institutions abroad. Private or endowed institutions, and even individuals, were included sometimes when it seemed that

they might have valuable data. The information reported from institutions in the United States and Canada was in general considerably more detailed and complete than that from overseas, but in the latter case there was not always sufficient time to prepare complete data. A great deal of work was required in filling out some of these survey forms, and the Department heartily thanks all who cooperated.

The preparation of the papers was assigned to Department scientists actively specializing in work with each kind or group of plants or animals. The authors have drawn on their own experience and knowledge, and on the whole field of technical literature, as well as summarizing the information obtained from the cooperative survey of plant and animal improvement. The only uniform rule adopted for the papers was that the material of most interest to the intelligent farmer or the general reader was to come first and to be put in language as nontechnical as possible. The more strictly technical material was placed last. Thus, after the principle successfully followed by Jack Spratt and his wife, the general reader may skip the brief technical section at the end of most of the articles if he wishes, and the technical reader may skip the first part of the article if he is so inclined. Basic data and tables, including lists of plants with superior germ plasm for various characteristics available for future breeding work, appear in appendices to the articles.

Though the genetic background and breeding techniques are essentially the same with a good many different plants, it will be found that some discussion of these aspects of the work has been repeated to a certain extent. Since each such discussion is related to a particular organism, however, it seemed best to let the repetition stand, partly for the benefit of readers who may be interested only in certain articles. Moreover, the subjects dealt with in the present book will appeal to a large number of gardeners, orchardists, beekeepers, and other enthusiasts or specialists who may have only vague notions about genetics, even when they carry on practical breeding with the plants or animals in which they are most keenly interested. In such instances a certain amount of repetition should be useful in making the basic facts understandable.

Four articles in the last part of the book—which some readers may prefer to read first—deal in greater detail with some of these fundamentals. The science of genetics is not a particularly easy subject, though its broad principles are not difficult to grasp, and anyone who wishes to go very far in plant or animal breeding must be prepared to undergo some mental discipline in the study of theory and technique if he expects to get all the facts straight. But for that matter, the details of the radio are not easy to grasp, either, yet there are thousands of capable radio amateurs who know a good deal about them. And in breeding work there is the advantage that the techniques involved, and the facts of genetics as far as they go, are at least relatively definite, which is more than can be said, for example, of the technique of writing good prose or poetry.

These concluding articles have been written with the lay reader in mind, but it will be found that they cannot be skimmed over like a detective story. On the contrary, they need to be read with the close attention that the detective in real life would give to some rather

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difficult technical evidence. For one of these articles we are indebted to A. F. Blakeslee, of the Carnegie Institution of Washington, who has been doing extraordinary things with the chromosomes of *Datura*, the genus to which our common jimsonweed belongs. Research in the field of unusual chromosome numbers is now attracting a good deal of attention among practical breeders because it suggests unique methods of creating new varieties and even new species of plants—that is, methods that are unique insofar as man is concerned, though it would seem that nature has used them from the beginning. For the chronology of genetics we are indebted to Robert Cook, editor of the Journal of Heredity, and to many of the leading geneticists and breeders in the United States, who critically examined his manuscript. E. N. Bressman has undertaken the difficult task of explaining some of the theory on which modern breeding practices rest; and J. R. Magness has dealt with the differences between vegetative reproduction and reproduction by seeds, which must be clearly understood in breeding work.

For a glossary of genetic terms the reader is referred to the 1936 Yearbook of Agriculture.

SUMMARY OF YEARBOOK ARTICLES

In the following pages all of the articles in the 1937 Yearbook are briefly summarized so that the general reader may quickly grasp the scope of the work as a whole.

Vegetable Crops—Introduction

In comparison with such major farm crops as the cereal, fiber, sugar, and forage plants, the vegetable crops are far more numerous, less understood genetically, and usually more limited to regional or national use. For example, superb English varieties of peas or cucumbers, or Italian varieties of tomatoes, either do not do well in this country or do not suit our habits and prejudices. In some countries Amercian sweet corn is not considered fit for human food; and on the other hand, many vegetables commonly eaten in Asia are unknown in the United States. Vegetable breeding, in other words, is a highly localized affair. We draw on the whole world for variant plant forms, obtained by the Division of Plant Exploration and Introduction in the Bureau of Plant Industry, but today these are used almost entirely as sources of genes for specific characteristics needed to strengthen and improve our own favorite types.

Systematic vegetable breeding by public agencies in this country is for the most part not more than 10 or 15 years old— in some cases, very much newer. Prior to that time, for decades and generations individuals and commercial firms had been busy producing better vegetables, largely by mass selection, with a little hybridizing here and there. Naturally, we owe most of our present varieties to the work of these men. The number of improved new forms introduced by public agencies is as yet very small, though in acreage they make a more respectable total. They will steadily increase. The kinds of problems that are pressing today, notably the urgent one of disease resistance, and the increasing complexity of the research needed for quicker and more certain results make the old haphazard methods

obsolete, excellent as they were in their time, and necessitate a well-organized scientific attack by public institutions. The commercial agencies in turn benefit by the work of these institutions. Seed certification in itself, though not directly connected with breeding, has been a State function of great value in holding the advances made by breeders.

Two new Federal institutions are of unusual interest and potential value. One is the United States Regional Vegetable Breeding Laboratory just established at Charleston, S. C., under the authority of the Bankhead-Jones Act of 1935. This is the only station in the United States devoted exclusively to vegetable breeding, and it will be concerned with basic problems affecting the Southeast. The other is the Great Plains Horticultural Field Station at Cheyenne, Wyo., where everything possible will be done to extend the meager list of vegetables now available for growing under the trying conditions found in this region.

There is a single appendix for most of the articles on vegetable breeding in the Yearbook, and this appendix includes work being done with some crops—sweetpotatoes and peanuts, for example—on which there was too little material to warrant separate articles.

Tomatoes, Peppers, Eggplant

As in the case of some of our literature and other native American products, Europe appreciated the tomato first, while Americans did not generally know that it was good to eat until about 1850, and the first improved varieties came from England and France. After 1870, commercial breeders in this country were active in selecting chance variants characterized by large handsome fruits, high yield, and plants adapted to local conditions. Among the leaders in this work was A. W. Livingston, of Columbus, Ohio. He and his associates were geniuses at selecting and perpetuating superior tomatoes. By 1910 there was a rich range of varieties, and the old methods are still used with some good results.

Chance variation is not certain enough, however, to meet the pressure of modern needs for resistance to disease, heat, and cold, and adaptability to long-distance shipment, new areas of cultivation, new processes and uses. Since 1910, there has been a more systematic attack on these problems by State and Federal workers, and a greater use of genetic analysis and controlled hybridization to meet them. Major attention has been given to resistance to fusarium wilt, but nailhead rust, leaf spot, leaf-mold, mosaic, and curly top have all had some attention. Practically speaking, no research agency today would introduce a new tomato unless it was resistant to at least one very troublesome disease.

Many State stations have done and are doing notable work in this field, and the list of new varieties is growing to respectable length. Federal workers have also been very active. The most important variety of tomato in the world today, Marglobe, was developed by Pritchard and Porte in the Department. Marglobe is highly resistant to wilt under most conditions and to nailhead under all conditions, and it came in time to save the Florida tomato-shipping industry from ruin. But Marglobe has faults too, and it will be superseded by

better tomatoes that will develop from the active research and experiment now going on.

Hot and sweet peppers, or chilis, also are native to tropical America. There has been comparatively little breeding work with these plants, and all the types grown today were known 200 or 300 years ago. A few enthusiasts among private breeders, however, have made improvements, particularly in uniformity, conformity to type, thickness of flesh, and earliness of maturity. The New Mexico and the Louisiana stations have introduced improved strains of hot peppers, and the Massachusetts and Connecticut stations have introduced early sweet peppers adapted to New England.

Even less systematic breeding work has been done with eggplant because of the relative unimportance of this crop in the United States. Native to the Tropics of the Old World, it has long been esteemed in some of the oriental countries. All the important varieties grown here were developed by private gardeners and seedsmen. The New Hampshire, Rhode Island, and Wisconsin stations are doing some breeding work for increased earliness, and the Central Experimental Farms of Canada have introduced an early productive strain of Black Beauty

A rather impressive amount of research has been done on the genetics of the tomato, but there is a great need for the development of more accurate tests to measure degrees of resistance to disease as a foundation for working out the inheritance of resistance. More basic information of this kind is needed if practical breeding is to achieve results with greater certainty. Of great theoretical interest is the newer work on forms with abnormal chromosome numbers—both triploids and tetraploids have been produced artificially There has been much less genetic and cytological research with the pepper and the eggplant In the case of the eggplant, Japanese workers have made some interesting studies of hybrid vigor and parthenocarpic fruiting (without fertilization of the ovules).

Cucurbits

Cucumbers and muskmelons are believed to have come originally from India and watermelons from tropical Africa. Pumpkins and squashes are of American origin. Columbus thoughtfully brought muskmelon seeds to North America, and in a few years native tribes from the West Indies as far north as Canada were growing melons. The early commercial and private breeders did their job so well with all these crops that some varieties originated over a hundred years ago are still popular among growers. Indeed, improvement by breeding today centers largely on fighting disease and spreading the climatic range of some of the cucurbits.

Cucumber growers suffer heavy losses from mosaic, downy mildew, and bacterial wilt. In the search for resistant varieties, plant breeders of the Department of Agriculture have found promising material among stocks from the Orient—China, Japan, India. Inbred lines of these show considerable resistance to mosaic and some resistance to mildew and wilt. Work is now in progress to introduce resistance into otherwise good American varieties by hybridization. At the Maine station, cucumber scab has received attention, and inbred

lines pure for resistance, as determined by artificial inoculation, have apparently been found.

The story of the development of our numerous melon varieties from material drawn from many parts of the world is a complicated and interesting one. The most striking work in disease resistance has been in connection with powdery mildew, which suddenly became a menace in the Imperial Valley, the chief muskmelon section of the United States, in 1925. By 1928 J. T. Rosa of the California station and I. C. Jagger of the Department of Agriculture had discovered resistant plants in material from India. Commercially useless, they were crossed with good American varieties, then backcrossed to the American parent variety to improve quality, and a resistant hybrid, of which Hale Best is one parent, was ready for use by 1932. Further backcrossing to Hale Best and 2 years more of selection brought the still better Powdery Mildew Resistant Cantaloup No. 45 in 1936. The mildew threat in this area has been beaten. Resistant strains of Honey Dew and Honey Ball are now being developed.

The California station has recently developed superior watermelons from the old Klondike and Stone Mountain, and from Russian stock the Minnesota station has bred a watermelon that can be grown farther north than others. The most serious watermelon disease is fusarium wilt. Within the last few years, the Iowa station has bred a number of resistant strains, and in 1936 both the Florida and the California stations released new wilt-resistant watermelons. It is interesting to note that the first recorded attempt to synthesize a commercial plant resistant to a particular disease was a hybrid between watermelon and stock citron (wilt-resistant but inedible), made by Orton of the Department of Agriculture and produced in 1911.

Squash breeding has had rather different objectives—the production of varieties superior in uniformity, earliness, quality, and appearance. This has been done chiefly by isolating superior lines among varieties rich in variable characteristics—a task that is facilitated by the fact that inbreeding generally has no harmful effect on cucurbits (and, conversely, crossing apparently does not result in hybrid vigor). The Vermont station has been a leader in this work. The North Dakota station has produced a squash of high quality in an attempt to create a substitute for sweetpotatoes in the northern Great Plains area. The California station and the Connecticut station at New Haven have recently introduced new squashes.

Some inheritance studies have been made with all the cucurbits, and interesting work has been done on reproductive responses, breeding behavior, and pollination technique, in all of which there are peculiarities not common to other plants.

Onions

The Israelites wandering in the wilderness complained bitterly to Moses because they had no onions. The unique, pungent flavor of onions makes them in no less universal demand today. Americans consume well over a billion pounds a year, worth $17,000,000 to growers—not counting the onion relatives, garlic, leeks, shallots, and chives.

Varieties have a rather strict regional adaptability partly because they refuse to produce 100 percent normal bulbs except with a certain definite length of daylight. One group will do this with a short day of 12 hours. Another requires a 13-hour day, and another 13½ hours. Yellow Globe Danvers demands 14¼ hours of daylight, and Sweet Spanish strain no. 2 still more. Extra-early varieties, like Bermudas, will not do well when seeded in the North because the day has already passed the minimum bulbing length by the time seed is sown. Late varieties will not do well in the South because when the day is the right length for bulbing, heat, sunscald, pink root, and thrips retard growth. These conditions can be changed when breeders develop varieties resistant to diseases and insects and adaptable to a wider range of climatic conditions.

The principal troubles of onions are pink root, smut, mildew, smudge, neckrot, yellow dwarf, thrips, and bolting (premature seeding). Until recently, there was little or no attempt to overcome these troubles by breeding. Today the prospects look very promising. One of the most valuable aids in breeding for resistance to various troubles may prove to be the Japanese onion, especially the Nebuka type. Nebuka onions belong to a different species than our onions, and they are of very little use commercially in the United States because they produce no bulbs. But they are resistant to various diseases, insects, and adverse climatic conditions, and by suitable crosses, these qualities can be transferred to American types.

Active work is in progress now in the breeding of hybrids with Japanese onions that are resistant to thrips, pink root, and smut. Work is also in progress in isolating strains of onions resistant to mildew. Resistance to smudge, it has been determined, is due to a certain acid associated with the pigment in yellow and red bulbs; whether the genes responsible for this acid can be incorporated into white onions remains to be seen. A substance in the outer scales of colored bulbs also seems to be poisonous to the fungi that cause neckrot. The Sweet Spanish variety of onion has been found to be very resistant to the virus disease, yellow dwarf. Resistance to thrips shown by certain varieties and species seems to be due to growth habits and leaf shapes that fail to offer protection to the insects; perhaps there are also other characters involved that help the plants to withstand injury. Certain varieties have been found to be highly nonbolting, and these are being crossed to produce nonbolting hybrids. Indications are that the same thing may be done to secure resistance to freezing injury.

With such facts determined, the breeder is in a position to carry on a well-directed program. Techniques of inbreeding and cross-breeding are well developed. The onion is normally cross-fertilized, and selfing results in rapid deterioration, but with care it produces pure strains for hybridization. In making difficult species crosses—as with Nebuka—flies are specially grown and let loose in a cage that covers the emasculated seed parent and also contains a cut flower stalk of the pollen parent.

The onion has been used in interesting studies to develop methods of identifying specific chromosomes under the microscope, and there has been some genetic analysis of the inheritance of color and of certain abnormalities in chlorophyll development.

Peas and Beans

Peas apparently originated in Ethiopia, and according to one authority they are the only vegetable that can with certainty be traced back to the Stone Age. They are also the first crop with which controlled breeding was done to produce new varieties (by Thomas Andrew Knight, 1787), as well as the plant used by Mendel in determining the laws of inheritance that founded modern genetics.

They reached their greatest perfection in England, and many American varieties trace directly to the splendid products of the famous English breeders, beginning with Knight, who introduced the first sweet wrinkled pea. The most highly evolved variety so far is probably Laxton Progress, which blooms at the eighth or ninth node and is therefore a few days earlier than its nearest competitor, Hundredfold—a characteristic that, to pea farmers, was worth years of breeding effort.

American breeders received their greatest stimulus from the canning industry after 1900. Slight differences in such characteristics as pod size, pod curvature, tightness of peas in pod, number of peas in prime condition at one time, node of first bloom, and straightness of stem have been important breeding objectives to achieve the closest possible adaptation to machine handling and other needs of the industry. In garden peas, the chief American contribution has been a great reduction in the incidence of the defect known as "rabbit ear." Today, preservation by freezing presents new objectives; and with all types of peas, American workers are now concerned with breeding for resistance to fusarium wilt and other diseases, as well as to insects and adverse weather conditions. Active breeding work is being carried on by several State experiment stations, notably Wisconsin, by the United States Department of Agriculture, and by some of the larger seed companies.

Elimination of strings was the chief objective of the early commercial breeders of snap beans, and the most successful among them was Calvin N. Keeney, of New York, who produced many varieties still popular, including Burpee Stringless Green Pod, Giant Stringless Green Pod, Stringless Green Refugee, and Brittle Wax. Later, the ravages of disease made it imperative to give major attention to breeding for resistance. New York State has led in breeding beans resistant to anthracnose. The Michigan, Idaho, and Wisconsin stations, the United States Department of Agriculture, and the Department in cooperation with the Wisconsin station, have produced varieties resistant to mosaic, and some of these are tolerant to bacterial blight. Strains resistant to bean rust have been bred by the Department and by the Virginia station. Thus the major bean diseases have been overcome to some extent, and the work is being actively carried on to make greater gains.

Little controlled breeding work was done with lima beans until a project was recently started in the Department. All the present varieties resulted from selection. Of the two most extensively grown today—Henderson Bush and Fordhook (also a bush lima)—the former was found on a Virginia roadside by a Negro laborer in 1885 and sold originally to a seedsman in Richmond, and the latter was

discovered growing in a field of pole limas in California in 1903. A hardy, high-yielding strain recently selected by the California station came from stock grown by the Hopi Indians.

Considerable genetic research has been done with peas, although this plant proved to be far more complex genetically than Mendel's early work would have indicated. To date, 68 genes have been listed. Research in bean genetics has also been extensive, and the inheritance of disease resistance has received, and is still receiving, a good deal of attention. Very little genetic research has been done with the lima bean.

Cabbage and Its Leafy Relatives

At least 4,000 years ago men were eating the leafy wild cabbage found on the coast of Europe and northern Africa; and this plant is supposed to be the original ancestor of such varied forms as the cultivated cabbage, cauliflower, broccoli, green-sprouting broccoli, Brussels sprouts, kale, collards, and kohlrabi. For our modern varieties of these vegetables we are largely indebted to farmers and to the assiduous work of commercial seedsmen, in both Europe and the United States, beginning in the late 1700's.

The most important single achievement in modern cabbage breeding in the United States has been the development of varieties resistant to yellows (fusarium wilt)-- an achievement that has saved growers from ruin in many sections and paid an enormous return on the cost. The problem was first attacked in 1910 in Wisconsin by L. R. Jones; and later J. C. Walker, of the Department of Agriculture, and his associates devoted many years to it. As a result of these intensive attacks, the wilt risk is now eliminated and there are yellows-resistant cabbage varieties of all the major types.

New varieties of cabbage that show improvements in other ways have been developed in Pennsylvania, Louisiana, and New York; and at several other State stations, as well as in the Department, breeding programs are in progress that promise worth-while results. The chief objectives today relate to diseases other than fusarium wilt, improved ability to hold up well in storage, better adaptation to particular localities, and a closer approach to consumer preferences, which favor a small or medium-sized hard head, mild or sweet in flavor, with crisp or succulent leaves.

Cauliflower and kohlrabi seed cannot be grown most successfully in this country, but broccoli seed can be, and new strains that mature at different times have been developed by private seedsmen in California. Green-sprouting broccoli has also been improved by breeding. New strains of Brussels sprouts have been privately produced in Oregon, and a new strain of kale has been released by the Virginia Truck Experiment Station. The Louisiana Station has introduced a new strain of collards.

One outcome of the breeding work with cabbage has been the development of interesting practical techniques for handling the plants and inducing the setting of seed under unusual conditions. Self-sterility is a problem with this plant, and as a result of intensive study much light has been thrown on the nature of self-sterility and self-incompatibility not only in cabbage but probably in other plants also.

Wide crosses between the cabbage and other species of the same genus have been fruitful in yielding cytological information, and there have been genetic studies of the cabbage concerned with the inheritance of characteristics of the leaf, the head, and the stem, as well as of plant height, bolting habit, season of maturity, and yellows resistance. Some work has been done on locating certain genes in definite chromosomes.

Root Vegetables

The turnip, rutabaga, radish, beet, carrot, parsnip, salsify, and taro are biennial plants, which means that they store a rich supply of food (mostly starches and sugars) in their roots during the first season to support growth during the second season, when they produce seed. Early in his history man learned to take this food supply for his own nourishment, just as he learned to steal the store of honey from the bee.

Over a long period of time improvements were made and definite types were set in these root crops by crude selection. Even in our own times, practically no other kind of breeding work has been done with them. But though the results of mass selection have in some cases been excellent—as with the carrot—the method no longer meets modern needs. In particular, the attacks of diseases and insects make it imperative to develop resistant types by the newer methods of inbreeding, crossing, and the introduction of valuable germ plasm from wild forms of these species.

There is very little work of this kind to report. On the other hand, there has been some interesting genetic research with these plants, and the unusual difficulties that some of them offer in breeding technique have been ingeniously overcome. The road has been cleared to some extent for going ahead with practical breeding programs based on definite objectives.

In order to "purify" the genetic make-up of a plant as a basis for combining desirable characteristics by crossing, it is necessary first to inbreed the plant. This is difficult in the case of some of the root vegetables. Turnips, rutabagas, radishes, and probably beets contain genes that make them sterile to their own pollen or pollen of certain other plants of the same variety. The mode of action of these genes has now been worked out. They are recessives and must be present both in the pollen and in the ovule to produce self-sterility. Their characteristics can be overcome to a considerable degree by applying pollen to a bud before it opens; or they can be replaced by "normal" genes through appropriate crosses; or naturally self-fertile lines can be discovered by enough searching and the others discarded.

In the case of the beet, the extreme dustlike fineness of the pollen, which can float in through tiny crevices, makes accurately controlled pollination difficult. This has been overcome by suitable techniques. The carrot was long thought to be self-sterile. Now it is known that the ovary merely develops before the pollen of the same flower is mature. Self-fertilization can readily be accomplished by using pollen from an older flower on the same plant. The flower parts are so minute that the usual methods of controlled pollination cannot be used, but this has been overcome by making flies do the work, inside special cages.

Along with such technical developments, research has uncovered facts about the inheritance of characteristics in these plants, some of which are of importance agriculturally—for example, bark and flesh color of turnip and rutabaga; color, corkiness, early and late flowering in the radish; color of root and top, and root shape in the beet; root color in the carrot. Investigation of chromosome behavior has also been fruitful. Certain wide crosses have been made, as between radish and cabbage, radish and Chinese cabbage, turnip and rutabaga, that may develop worth-while breeding possibilities.

Salad Plants

Since the public became vitamin-conscious, the salad crops—lettuce, celery, endive, chicory, cress, and parsley—have increased in importance. Very little scientific breeding work has been done with any of these plants except lettuce and celery, the major salad crops. The production of both is confined to rather specialized areas. Lettuce, one of the oldest vegetables grown, came originally from India or central Asia and was introduced into the United States early in the colonial period. Celery, native to the Mediterranean region, was long considered to be poisonous and has been eaten only in modern times.

Lettuce breeders have several solid achievements to their credit. Most notable of these is the development of the Imperial strains by I. C. Jagger, of the Department of Agriculture. This work was started in 1922 to meet the combined threat of brown blight and powdery mildew, which were on the point of wiping out growers in some of the largest western producing sections. The resistant Imperial strains, developed by hybridization, saved the industry in these areas.

Since transportation developments made possible the shipment of western lettuce to the East, eastern consumers have preferred the crisp western type. The present varieties of this type cannot be grown well in the eastern climate. A start was made in 1928 toward developing crisp-head types for eastern growers, and the first of these, Columbia No. 1 and No. 2, were released by the Department in 1936. A wholly new type of lettuce, Cosberg (a cross between Cos or romaine and Iceberg) was also introduced in 1936. This is comparatively free from tipburn, which is very troublesome in the East. The Department is now cooperating with several eastern State stations for the development of other crisp types adapted to local conditions.

Tipburn and mildew are both serious in greenhouse forcing. The Ohio station has developed a tipburn-resistant strain of Grand Rapids, and the Massachusetts Station a butter-head type, Belmay, resistant to mildew.

Celery growers need earlier maturing plants and plants resistant to yellows, premature seedstalk development (bolting), and pithiness. Breeders have been attacking these problems. Michigan released its Michigan Golden Yellows Resistant celery in 1933 and its Curly Leaf Easy-Blanching (also yellows-resistant) in 1936. A new Non-Bolting Golden Plume has been introduced by a private seed concern in California. Pithiness has now been proved to be an inherited characteristic, which paves the way for breeding nonpithy strains.

Although lettuce flowers are difficult to handle in breeding operations, some genetic studies have been made on the mode of inheritance of various characteristics, including plant height, time of flowering, habit of growth, length, width, and area of leaves, and particularly color. Genetic studies in celery indicate that pithiness is due to a single dominant gene, and that bolting may also be a dominant characteristic controlled by several genes but greatly influenced by environment.

Sweet Corn and Popcorn

Some of the greatest advances in breeding technique in recent times have been made with field corn—in particular, the method of crossing certain inbred lines to produce a hybrid that has remarkable uniformity and productiveness. These advances have naturally been reflected in sweet-corn breeding also.

Two outstanding needs have dominated breeding work: (1) The canning industry requires stocks that are as uniform as possible in every way, besides having high yield. (2) The fact that sweet corn cannot be grown in the South, largely because of the ravages of the corn earworm and of bacterial wilt, makes it highly desirable to develop resistant varieties.

Breeders have met the first need so effectively with the newer types of hybrid corn that the canning industry itself has been revolutionized by the uniformity in texture and consistency of grains and the uniformity of ripening in the field. Whole-grain canned corn, frozen packs, and new machinery have been made possible by the work of breeders. About 80 percent of the yellow sweet corn grown for canning now consists of the newer hybrids, and about half of this is Golden Cross Bantam, a product of the Department in cooperation with the Indiana station. Other States that have led in recent breeding work have been Maine, Illinois, Connecticut, and Minnesota. Not the least of the advantages of Golden Cross Bantam corn is its resistance to bacterial wilt.

Promising work is in progress to meet the second major need—extension of the sweet corn region southward—by hybridizing sweet corn with the naturally earworm-resistant dent field corns of the South. The factors that make this dent corn resistant to the earworm have not yet been satisfactorily determined, but varieties developed from sweet-dent hybrids like Honey June and Surecropper Sugar have more resistance than any other sweet corn. Leaders in this work have been the stations in Texas, Florida, Georgia, and California. Truck and home gardeners in the South are keenly interested in these efforts.

The characteristic kernel composition of sweet corn, which distinguishes it from field corn, depends on a recessive form of the gene for starchiness. The presence of this recessive prevents the conversion of some of the sugar into starch. A good deal of work has been done on inheritance in sweet corn.

Popcorn pops because the horny endosperm in which the starch grains are embedded confines the steam generated by heat until it develops sufficient force to explode the kernel. Popcorns differ in popping expansion, and the differences can be easily measured. They also differ in tenderness and flavor of the popped kernels, productive-

ness, and resistance to diseases and insects. Fortunately high poppability and tenderness seem to go together, but unfortunately high poppability and productiveness do not, so that in breeding a compromise is necessary between these two characteristics.

Breeding work with popcorn has been relatively limited, but it has produced some promising results. Mass selection, based on actual popping tests or on a rough comparison of the amount of soft white starch in kernels (the more starch, the less popping expansion) is useful in bringing about a gradual improvement in popping expansion, at least up to a certain point. The improvement in a 6-year experiment conducted by the Department in cooperation with the Kansas station was about 36 percent, and the improved strain has been distributed as Supergold. Hybridization of inbred lines has been carried on by several stations. At the Minnesota station, 250 lines of a selection of Jap Hulless were developed by inbreeding, then culled to 7 lines by selection, and all possible crosses were made among the 7 lines. One cross was selected as superior; the hybrid, named Minhybrid 250, has had a 16-percent higher yield and a 29-percent higher popping expansion than the Jap Hulless used for comparison. A continuation of this project with new inbred lines is now in progress in Minnesota. At the Iowa station, a promising three-way hybrid is now under test, and a group of inbreds is in the developmental stage. In a cooperative project between the Department and the Kansas station, 81 hybrids have been produced recently, of which about one-fourth show some improvement in popping expansion, and almost 90 percent show a marked improvement in yield. The Michigan station is now carrying on an interesting experiment in producing synthetic varieties by combining a fairly large number of inbred lines.

Injury caused by diseases and insects is a distinct drawback in commercial popcorn. In the case of some diseases, selection for commercial characteristics tends also to bring about some selection for resistance. In the Southern States particularly, damage from the corn earworm and from storage insects is serious. The Texas station has a project under way in which an attempt is being made to introduce the insect resistance of their adapted field corn varieties into popcorn of good popping quality.

POTATOES

Native to cool regions in South America, potatoes were taken to Europe by early Spanish explorers and grown there for a hundred years before they were introduced into the New England colonies from Ireland (1719, Londonderry, N. H.).

For another hundred years, little improvement was made in varieties. Then there was a rush to produce better potatoes. A minister, Rev. C. E. Goodrich, of Utica, N. Y., laid the foundations for potato breeding. He thought the ravages of late blight were due to loss of vigor through long vegetative reproduction by tuber cuttings, and he proposed to restore vigor by growing plants from seed. Some 170 varieties can be traced back to a single one of his seedlings, Garnet Chili. C. E. Pringle, of Charlotte, Vt., was the first to make systematic attempts to obtain seed by controlled hybridization.

In the United States today, potato breeding is extensive and well organized under a national potato-breeding program. Under this program, the Department coordinates the work in 13 States that are carrying on active breeding projects, with 21 States cooperating in testing worth-while material developed in these projects. Regional problems are considered, and States in which seed cannot be grown obtain it from States in which it can be grown. The various Department field stations and State agricultural experiment stations stress different aspects of the general problem, but altogether practically every aspect of potato breeding receives attention, including disease resistance, yield, adaption to locality, earliness, tuber shape, smoothness (depth of eye), cooking quality, breeding methods, genetic analysis, and study of chromosomes.

The breeding methods include the full range of those used in modern plant breeding—the introduction of new varieties or species, selection of colonal lines, crosses between varieties, brother-sister crosses (sibmating), backcrosses to parents, selfing and the recombination of selfed lines (as in the breeding of hybrid corn), outcrossing to unrelated strains, the synthetic building of strains by a combination of various methods, and wide crosses between different species (as between a cultivated and a wild form).

The outstanding problem is resistance to diseases, including a whole group of virus diseases, late blight, common scab, fusarium wilt, rhizoctonia, early blight, blackleg. These diseases add enormously to growers' costs. Late blight, the most important, has caused losses of 9,000,000 bushels of potatoes a year for the last 10 years; in 1928, the loss was 28,000,000 bushels. The severest possible tests for resistance are given, and so far very promising progress has been made in the development of many varieties resistant to late blight, a large number resistant to scab, a large number resistant to mild mosaic, and one variety and several of its progenies immune from latent mosaic. The search for disease resistance will be continued until every possibility has been exhausted.

From a practical standpoint, six new varieties have been named and distributed in the last 5 years (Katahdin, Chippewa, Golden, and Houma by the Department; Warba and Red Warba by the University of Minnesota). Another, not yet named, is being tested by farmers. Katahdin and Chippewa are now firmly established as commercial varieties.

With a wealth of available breeding material, breeding methods well tested, considerable genetic and cytological information, and a planned cooperative program, potato breeders are in a position to expect further progress with confidence.

Strawberries

The strawberry is not of ancient lineage as a cultivated fruit, though the Indians of Chile were growing remarkably fine selections of the wild beach strawberry before the time of Columbus. Five plants of this type reached France in 1714, and these were crossed with the wild meadow strawberry of eastern North America, which had previously been taken to Europe. The result was a vigorous hybrid, the modern cultivated strawberry—a European creation out of Ameri-

can parentage, so welcome and adaptable that it is now grown from Alaska to New Zealand.

Since the strawberry is relatively so new, most of our varieties are products of breeding, though a few have been found as chance seedlings in the wild. These are natural hybrids of cultivated and wild berries, for many of the wild sorts now contain chromosomes obtained from the pollen of their cultivated neighbors. Extensive commercial production did not begin until after the Civil War, when the first firm-fruited variety, Wilson, made strawberry growing in the South possible. Today, 20 varieties created in the last 45 years (Gandy, the oldest, in 1885) account for over 99 percent of the total acreage, and 6 of these (Klondike, Howard 17, Aroma, Blakemore, Missionary, and Marshall) for 78 percent. Most of the 20 varieties were produced by private breeders, and several famous private breeders of outstanding varieties are still living and carrying on their work.

Systematic strawberry breeding is now being carried on by the Department and by the agricultural experiment stations in 26 States, as well as in Alaska and Hawaii. Hundreds of thousands of seedlings are constantly being grown, of which perhaps two in a hundred are selected as worthy of a first fruiting test, and a very small percentage pass the final rigid test and are named and introduced. At many of these stations the work is new and has not yet had time to produce results. The Department has released 7 varieties, Minnesota 16, New Jersey 1, New York 21, North Dakota 1, Oregon 1, South Dakota 2, Tennessee 1, and Alaska 1. Strawberry growers readily adopt improved varieties, and such new introductions will account for an increasing acreage in the future. Breeding work is also actively carried on in Canada, England, Norway, Sweden, Germany, Switzerland, Czechoslovakia, the Union of Soviet Socialist Republics, Japan, and Australia.

The usual method of breeders is to cross varieties and species and backcross to the parents. The newer method of inbreeding and combining inbred lines has been used very little, partly because the strawberry plant loses vigor so rapidly with inbreeding. This method will very likely be necessary, however, to eliminate recessive genes that probably account for susceptibility to certain diseases as well as for other weaknesses. There is considerable confidence today that the excellent characteristics of many varieties and of the three wild 56-chromosome species (meadow strawberry, beach strawberry, Rocky Mountain strawberry) can be combined in a few outstanding types suitable for the wide range of strawberry-growing regions. Broadly, the objectives today are greater resistance to several diseases, and possibly to insects and nematodes; greater resistance to high temperatures, low temperatures, and drought; better adaptation to long and short days; better dessert quality under adverse weather conditions; increased firmness and toughness of skin; and better adaptation to certain specific uses such as canning, preserving, freezing, and flavoring.

Fundamental research with the strawberry has been concerned with the inheritance of a few contrasting characters and with chromosome behavior, largely in crosses between species with different chromosome numbers.

Blackberry and Raspberry

By clearing the forests, Americans set up a vast natural blackberry breeding project, for in the clearings the sparse growth of blackberries became dense, and since all blackberries need cross-pollination, a multitude of natural hybrids arose. For the last 75 years or so we have been making selections from this pool of mixed germ plasm, which has been the source of almost all our commercial varieties, including Lawton, Eldorado, Snyder, and the dewberry or trailing blackberry Lucretia. However, in the West the Logan (Loganberry) came from a cultivated variety, the Young dewberry (Youngberry) is an artificially produced hybrid, and the Evergreen (Black Diamond) and the Himalaya are of European origin. Whether the Logan is a blackberry-raspberry hybrid is still in dispute.

Comparatively little systematic breeding has been done with blackberries by public agencies, but the Department and several of the State stations are doing some work. There is much interest in developing thornless varieties. This has been accomplished several times by the use of mutations, but unfortunately only the outer layers of the plant tissue carry the characteristic of thornlessness, and new plants developing from the inner layers—as they do in the case of root cuttings—are all thorny. Also, thornless plants generally tend to be sterile. Other major practical objectives in breeding are superior hardiness, productiveness, vigor, flavor, firmness, and size; smaller seeds; and resistance to diseases, nematodes, and drought. Many crosses have been made by the Department and by the New York, Rhode Island, and Texas stations, and a few improved varieties have been introduced as a result. Workers at the Texas station, and in England, have been especially interested in experimenting with blackberry-raspberry crosses, but none of these has as yet produced a worth-while commercial variety.

Both European cultivated red raspberries and selections from native wild varieties were probably grown in the United States before 1800, but the red raspberry did not become commercially important until after 1865, when an industry was founded on the famous Cuthbert variety, discovered as a chance seedling in New York. The best cultivated red raspberries were developed by definite breeding work, mostly by the State stations, far more than has been the case with blackberries, and since this work began a considerable number of superior varieties have been introduced, including such important ones as Latham, Chief, Ohta, King, and Viking.

Breeding work is being actively carried on by the Department and the experiment stations in New York, South Dakota, Illinois, Washington, Minnesota, Tennessee, and North Carolina, and many thousands of seedlings that have resulted from crossing and selection are being tested. This includes work with the black and purple raspberries, crosses between red and black and between American varieties and Asiatic species, and the development of fall fruiting or everbearing forms and of varieties adapted to special purposes. Among other results are the production of berries bigger than would have been thought possible 10 years ago, and considerable success with varieties able to resist or escape major diseases.

But there are still great possibilities for improving the red raspberry, notably by bringing together in a single combination some of the superior characteristics now found separately in cultivated American and European varieties. Moreover, a large number of wild varieties exist in Asia and elsewhere, with extremely varied characteristics of plant and fruit, that the breeder has hardly yet begun to use in his programs. New possibilities will undoubtedly develop as these are more systematically explored.

Currants and Gooseberries

White-pine blister rust is not passed from pine to pine; it goes from pine to currant or gooseberry and then back to pine. This is unfortunate for currants and gooseberries; they have had to be wiped out in a good many places to save the pines. Extension of the now greatly reduced acreage will depend largely on the development of resistant varieties.

There are two kinds of currants, red and black. Of the red currants, five species, native to Europe and Asia, are considered especially important for breeders, and most of the leading American varieties (Fay, Wilder, Red Cross, Diploma, and Perfection) came from two of them. These American varieties were developed between 1877 and 1887 out of material that had been coming from Europe almost since the first settlement of New England. The European black currant is useless for this country because of its high susceptibility to blister rust, but the American black currant—which also has golden or white forms—is more resistant. Four improved American black varieties (Tonah, Atto, Mato, Wanka) were introduced by the South Dakota Station in 1925.

Very little systematic breeding work has been done with currants by either State or Federal workers. The South Dakota station has worked with black varieties; a number of crosses have been made and are being studied in New York; Minnesota has recently introduced a red selection, Red Lake; and Federal workers have made some crosses and selections but have introduced no varieties as yet. The most promising rust-resistant variety is Viking, an introduction from Norway. It seems in fact to be immune and is now being extensively tested by the Department cooperating with State stations. There are promising possibilities in breeding work with currants, especially the hardy, drought-resistant, vigorous American black varieties.

Greater promise, however, lies in the work with gooseberries. The greatest development of this fruit has been among the English, who became connoisseurs of gooseberries, held gooseberry shows, and offered prizes that stimulated breeding work, especially for large size. In the United States, gooseberry growers were discouraged by mildew until after 1900, when fungicides were used to control the disease. The most important gooseberry in this country has been Downing, a mildew resistant variety introduced about 1855. Poorman (1896) is the largest American-European hybrid. About a dozen species native to the United States are promising for breeders. They have a wide climatic range and such valuable characteristics as resistance to mildew, leaf spot, and high summer temperatures. These characteristics need to be combined with the great size, fine flavor, and attrac-

tiveness of European varieties, and some of the hybrids developed show the possibilities.

Breeding work has been carried on by several State stations. The South Dakota station has made crosses between a native wild species and European varieties, and these have resulted in some dozen introductions. The North Dakota station has recently introduced three varieties from crosses and is studying the inheritance of important characteristics. The New York station at Geneva has introduced one variety, and the Minnesota station has introduced an improved variety. The Illinois station is working for greater production, larger size, higher flavor, fewer thorns, and resistance to leaf diseases. The Department is doing some selection and hybridization, and has recently introduced one gooseberry, Glenndale, adapted to the upper South.

The breeding of both currants and gooseberries has been actively carried on in Canada, and in England research work has proceeded far enough so that the use of X-rays to induce mutations is now being studied. Breeding work is also being done in Sweden and in the Union of Soviet Socialist Republics.

Unusual Bush Fruits

All cultivated plants came originally from the wild, but only the most outstanding or the most adaptable have been extensively grown by man. Others from which men gather food might be adapted to cultivation and improved by breeding, just as the wild blueberry has been adapted and improved in recent years. Among the plants useful for landscaping there are also a number that might yield new forms or be made more valuable in other ways, if breeders would give them systematic attention. For example, columnar deciduous trees other than the Lombardy poplar might be created by breeding and would be extremely useful.

A few ornamental plants whose fruit is promising as food have received some attention. The actinidias (Chinese or Japanese gooseberries) are climbing shrubs bearing fruit up to the size of an egg, with a texture like that of a fresh fig, edible fresh or as a jelly or a cooked sauce. A single vine may produce several bushels of fruit in some years, but the need is to develop types that will bear regularly. The American cranberrybush or highbush cranberry (a close relative of the elderberry) produces fruit that makes a highly colored jelly of strong flavor. Several State experiment stations have cooperated with A. E. Morgan and the Department in improving this fruit by breeding, and three varieties are now available commercially. The goumi, or *Eleagnus*, has a tart fruit that is good in sherbets and is of considerable importance in central Asia. The plant is hardy and drought-resistant and might well be improved by breeding. The fruit of the oriental or flowering-quinces (Japanese quince is a common form) is extremely useful for jellies and preserves in combination with other fruits because it is rich in pectin and contributes an agreeable acid flavor. By breeding, it should be possible to develop larger fruit, with more acid and pectin and better color, which would be of great value in the preserving industries. The Chinese bush cherry (Manchu or Nanking cherry) is now receiving attention for its fruit,

which has an attractive tang and an agreeable range of flavors and textures. This fruit too has commercial possibilities, and some breeding work has been done with it in Iowa, New York, and Massachusetts.

Blueberries

Only a short time before his death on January 9, 1937, Frederick V. Coville completed an article for this Yearbook describing his work in developing the cultivated blueberry from the wild blueberry. Dr. Coville served 49 years in the Department of Agriculture, and probably his work with blueberries will stand out as the most important achievement of a fruitful career. It founded a new and thriving industry.

The work began in New Hampshire in 1906 with a study of the fundamental facts in the life history of the wild blueberry. The first fact established was one not before known—that blueberries, rhododendrons, azaleas, the mountain-laurel, and many other plants require acid soils.

Next, methods of grafting, budding, division, layering, propagation of twig cuttings and root cuttings, and pollination were worked out.

Then plants with superior fruit were chosen for breeding experiments. The first one, a highbush blueberry found in a pasture in Greenfield, N. H., was named Brooks. To the excellence of this first berry, Dr. Coville attributed much of the success of many of its later descendants. Efforts were made to self-polinate the Brooks, without success, and after other attempts, this method was abandoned in favor of cross-pollination. Much later, it was found that in cross-pollination, chromosome numbers were all-important. Even distantly related plants with the same number of chromosomes would cross, but if they did not have the same chromosome numbers, the cross yielded no fruit.

The second wild blueberry chosen was Russell, also from New Hampshire. In 1911 this was crossed with Brooks, and some of the first-generation hybrids were crossed with each other. Among 3,000 second-generation progeny, there was much segregation for various characteristics.

Thereafter, Dr. Coville made an intensive search for superior wild berries, enlisting the cooperation of Elizabeth C. White, of New Lisbon, N. J. Up to the year 1936 about 68,000 pedigreed blueberry seedlings were fruited and carefully tested for superior characteristics of bush, size of fruit, ease of picking, size of scar when picked, size of calyx, keeping quality, firmness, tendency to crack, and flavor. Taste tests were especially exacting and, with the consumer in mind, Dr. Coville would release no variety, no matter how remarkable its size or how good its other commercial characteristics, unless its flavor met his standards.

The largest berry developed in this work had a diameter of more than 1 inch, but it was not released because of inferior flavor. A hybrid between this and the finest-flavored berry, Stanley, has so far reached a diameter of nearly 1 inch. It is not yet ready to release, but Dr. Coville named it Dixi. His article describes the characteristics and ancestry of all his improved varieties—Pioneer, Greenfield, Cabot, Katharine, Rancocas, Jersey, Concord, June, Scammell, Stanley, Redskin, Catawba, Wareham, Weymouth, and Dixi.

Apples

To evaluate a new apple variety takes 25 years from the time the cross is made, and another 5 to 15 years will elapse before it is in commercial production. Practically speaking, the apple breeder works for his descendants, not for his own generation. Therefore as yet few of our widely grown varieties are the result of systematic hybridizing, even though this work was under way in 1895. Most of them came from superor chance seedlings. Apples were brought over from Europe by the early colonists, the seeds were widely disseminated, and since apples do not come true from seed, the range of differences in tree and fruit was very great. In fact this process extended back into early times. Primitive man appreciated the wild apple, though it was a wry thing, and he early began selecting and cultivating it. Budding and grafting were practiced over 2,000 years ago.

Today we need fruit with quite definite superior characteristics, and the hope of obtaining it lies in the extensive breeding programs of the present and the future. What are the objectives? Increased winter hardiness, of first importance in northern regions; disease resistance (the major diseases are scab, blotch, bitter rot, fire blight, and apple cedar rust); resistance to spray injury; late blooming to escape spring frosts in some sections; a combination of rich-flavored fruit with desirable tree characters (disease resistance, etc.); a greater range of fruits with high color and quality combined with ability to keep well in storage; varieties adapted to the far South—at present there are none that are satisfactory.

There is sufficient variation among the many different kinds of apples to give assurance that many of these desirable characters can be brought together in new varieties.

Three methods are available to bring about these improvements: (1) Keeping a careful watch for bud mutations; this has been practiced rather intensively during the last decade, and some very superior strains have resulted. The method is still highly promising, though it is limited to a relatively narrow range of improvement among existing varieties. (2) Hybridization to produce really new varieties by combining different characteristics. In some cases it is possible to go rather far afield; hardy crab apples are being crossed with commercial varieties of apples, for example, to get extreme cold resistance. (3) Producing varieties with unusual chromosome numbers. It happens that about 25 percent of our commercial apple varieties are triploids—that is, they have three full sets of chromosomes in their body cells instead of the normal two sets. Always these triploids have unusually large fruit and a vigorous type of tree; that is why so many of them happen to have been selected as superior. But the occurrence of triploid apples is very rare in nature, and so far it has been impossible to create them by controlled breeding methods. This is a secret that the apple breeder is trying intensively to solve.

Breeding projects are under way at the experiment stations in several States, and tens of thousands of seedlings are under test. So far, the Iowa station has introduced 13 named varieties; Minnesota, 5; Missouri, 7; New York, 15; South Dakota, 17. Work is also in progress in Idaho, Illinois, Maine, Maryland, Massachusetts, Ohio,

and Virginia, and the Department is doing a limited amount of breeding. A major program has been carried on in Canada, and apple breeding is combined with the breeding of other fruits in several European countries.

PEARS

Europeans have the same fondness for pears that Americans have for apples, and a great many delicious varieties have been developed in Europe. A Belgian physician, Von Mons (1765–1842), had as many as 80,000 seedlings in his gardens and developed over 400 varieties. At least as early as 1794, however, pears in the United States met the nemesis that has dogged them ever since. This is fire blight, a bacterial disease that attacks roots, crown, trunk, limbs, blossoms, and fruit. It is ruinously virulent in most of the East; in the West, relatively cool dry summers make it less destructive; but even there, it is a source of great trouble and expense to growers, since the only known method of control is by careful surgery.

Thus the fire blight menace dominates pear breeding in the United States. The European pear, source of all the fine-fleshed, buttery, melting, aromatic varieties such as Bartlett, Anjou, Bosc, and Winter Nelis, is especially susceptible. The Chinese or sand pear, coarse, gritty, and inferior, is resistant. Around the middle of the last century, hybrids between the European and the Chinese pear began to appear—Le Conte and Kieffer, for example. Although these are inferior in quality, they are about the only pears that have enough blight resistance to be grown in most parts of the East. One pear apparently of straight European parentage, the Seckel, is also resistant.

The problem, then, is to develop a wider range of the superior European varieties with resistance to the disease, either by hybridization or by selection. The most important basic breeding material includes the European pear (generally susceptible but with occasional resistant forms), the snow pear of southern Europe (susceptible), the Chinese or sand pear (variable resistance), the Ussurian pear of China and Siberia (very resistant, and especially valuable because the quality is fair), the Callery pear of China (resistant), the birchleaf pear of China (variable resistance). There is enough range in the available material to meet all requirements, including superior winter hardiness, which is needed in some parts of the country; but it may be another hundred years before the problem of fire blight is really solved, considering the length of time it takes to test a single generation of tree fruits.

The Oregon Station has led in this work. There F. C. Reimer has tested the resistance of practically all known species and varieties of pears, and of many hybrids, using artificial inoculation as well as natural infection. One of the most valuable breeding stocks is a highly resistant Anjou seedling called Farmingdale, found accidentally on a farm in Illinois. Ten other very resistant Eurpoean pears have been found in 10,000 seedlings, and all transmit a high degree of resistance in crosses.

The Department has also carried on fairly extensive breeding work for blight resistance, and 5,000 seedlings, inoculated each year, are now being grown to fruiting. Work has also been done in California (for range of ripening season), Georgia (studies of resistance), Iowa

(winter hardiness), Maryland, Michigan, Minnesota, New York (primarily for high quality and long ripening season), and Tennessee. Some new varieties have been introduced as a result of this work.

A limited amount of work has been done on the cytology and genetics of pears, but inheritance studies are difficult because selfing is impracticable in most varieties.

Grapes

Obedient to official urging and command, the early colonists in the eastern United States planted grapes of the traditional fine European varieties. All of these ventures failed miserably; the European varieties could not stand the diseases, the insects, and the cold that faced them in this part of the new land. In California, however, they throve ever since they were introduced by Mission Fathers from Mexico in 1769, and after 1850 grape culture in that State grew with great rapidity. Meanwhile, tardily, easterners began to become aware of the value of their own native grapes, which grew abundantly in the wild. Three chance seedlings—the Cape (believed to be identical with Alexander), discovered in 1806; the Catawba, first propagated in 1819; the Concord, named and introduced in 1854—had sufficient merit and popularity to turn the attention of breeders to these native species. Thereafter several men did notable work in selecting native varieties and hybridizing them both among themselves and with European grapes. Outstanding among these early workers were E. S. Rogers (Agawam), A. J. Caywood, Charles Arnold of Canada, G. W. Campbell (Campbell Early), Louis Suelter (Beta), J. H. Ricketts (Downing), and T. V. Munson, who originated more hybrids than any other man in the country.

Thus American grape growing has had two distinct lines of development. On the Pacific coast (especially in California), where 90 percent of the commercial grape culture is centered, European varieties are grown for the production of table grapes, raisin and currant grapes, and wine grapes; throughout the rest of the country, native varieties, hybrids between these, and hybrids with European varieties are grown for table grapes, wine grapes, and unfermented-juice grapes (the foxy flavor of the Concord, which is a fox grape, is important for this last use). Even the European grapes in California, however, must be grafted on native American rootstocks, which alone are resistant to phylloxera, an American insect that, finding its way to Europe, compels European growers also to use American grapes as rootstocks.

Grape breeding is actively carried on by the Department and by the State agricultural experiment stations in California, Georgia, Maryland, Minnesota, Missouri, New York, South Dakota, Texas, and Virginia. Many thousands of seedlings from an immense number of crosses are being grown and tested, and improved varieties have been released by the Georgia, the New York (Geneva and Fredonia), and the South Dakota stations. The general objectives in this work are improved fruit quality, disease resistance, and local adaptability; but there are separate objectives for the three main types of grapes. Thus, for American native bunch grapes it is desirable to have larger clusters and berries; some of the rich vinous flavor of the European grape; more edible skin, more melting flesh, seeds more free from the

pulp, increased sugar content. For the native muscadine grapes of the South, it is desirable to have larger bunches, better adherence of berry to stem, more tender skin, better flavor, smaller seeds. For the European grapes, it is desirable to have among the table types, more seedless varieties and a larger assortment of black, red, and white grapes ripening from early to late; among the raisin types, several improvements to meet specific needs; among the wine types, improved flavors (perhaps a blend of several flavors for certain kinds of wine), juice of better color, vines resistant to phylloxera to eliminate the necessity for grafting.

Needless to say, grape-breeding work is also being actively carried on in foreign countries, notably France, Germany, Italy, Czechoslovakia, the Union of Soviet Socialist Republics, and Australia.

Genetic analysis is slow, and there is need for more information on the inheritance of characters of importance, especially resistance to diseases.

Stone Fruits (Peach, Plum, Cherry, Apricot)

Grown in China thousands of years ago, the peach early spread throughout Europe and was brought to North America by the colonists; but commercial growing did not begin here until the nineteenth century, when orchards propagated from cuttings were first established. Between 1850 and 1900, peach growing became highly specialized, and to meet the need for types suited to different regions many varieties were developed by seedling selection, including such present stand-bys as Hale Early (1850), Belle and Elberta (1870), Crosby (1876), Champion (1880), Carman (1889), Rochester (1900).

Today, systematic breeding by hybridization is conducted by the Department of Agriculture and by the agricultural experiment stations in California, Illinois, Iowa, Maryland, Massachusetts, Michigan, New York, New Jersey, Texas, and Virginia, as well as in Canada. Many of these have only started recently, but the Department has introduced 4 varieties (1935), New Jersey 18 (1925–34), California 1 (1933), Iowa 1 (1932), Michigan 1 (1932), and Canada 6 (1925–30). The extent of some of this work can be realized from the fact that the New Jersey Station maintains 276 varieties of peaches and nectarines (a smooth-skin peach) on its breeding grounds for study and hybridization.

Objectives, of course, are different at different stations, depending on regional requirements and on the use for which the crop is intended. In general, there is still a need for a variety of high quality adapted to cold climates, and one that will not delay coming into leaf in climates where the winters are warm. Better varieties than Elberta—the best commercial peach so far—have been produced, but they are not so widely adapted. Promising hybridization work is now in progress with the Crawford type, which has very high quality, and with the J. H. Hale. A good deal of interesting genetic work has been done with the peach, but there is need for more.

Of the many species of plums native to various parts of the world, four are especially important commercially in the United States—the European plums, brought over by the first colonists, large, attractive, green and golden yellow (Reine Claude) to red and dark purple (Italian prune); the damsons of the Old World, yellow (Mirabelle) to blue

(Shropshire), small, tart, used for preserves; the Japanese plums, introduced into this country in 1870, yellow overlaid with red (Kelsey, Burbank), excellent flavor; the native American plums, especially the *Prunus Americana* species (De Soto, Weaver), red to reddish orange, good quality but a thick, tough skin and clinging pit. These species are rich in varieties available as breeding material, and there are also many other interesting species.

Several private breeders have done notable work with plums, including H. A. Terry and C. G. Patten, of Iowa, and J. W. Kerr of Maryland, who were interested in the selection of native varieties; Luther Burbank, who selected and hybridized Japanese plums and other species; Millard W. Sharp and A. F. and August Etter, of California, who are now engaged in hybridizing.

Much systematic hybridizing, both among the plum species and between plums and other stone fruits (cherry, apricot) is being conducted by State stations in California, Iowa, Minnesota, New York, and South Dakota, and by Federal field stations in California and North Dakota. Where the work has been longest in progress, as in South Dakota, New York, and Minnesota, several varieties have been introduced; elsewhere, promising material is still under test. The growing of plums has been declining in the United States during the last 20 years, and there is a great need for the breeding of varieties of really high quality adapted to regions characterized by extremes of heat or cold.

There are two species of cultivated cherries, the sweet and the sour. Sweet cherries are subdivided into two groups—heart or gean cherries, soft, tender, either dark colored (Black Tartarian) or light (Coe); and bigarreaus, firm, crisp, either black (Bing) or light (Napoleon). There are three groups of sour cherries—the amarelles, light (Montmorency); the morellos, dark (English Morello); and the marascas, native to Jugoslavia, used for making maraschino cherries. Duke cherries (May Duke) are probably hybrids between sweet and sour species Other species useful in breeding include the Nanking cherry of Asia; the sand cherry, the western sand cherry, and the chokecherry of the United States; and the mahaleb cherry of Europe and the pin cherry of North America, used as rootstocks

Commercial production of sweet cherries is practically limited to the Pacific and intermountain States, and that of sour cherries to regions along the Great Lakes The trees are too tender for colder regions; they do not thrive in hot, dry regions; and in hot, humid regions cherry diseases are disastrous. Breeding work is very much concerned with overcoming these major handicaps and making this delicious fruit available over a much greater area, and also over a longer season.

There has been little work by private breeders, though the development of black bigarreau varieties (Republican, Lambert, Bing) by the Lewelling brothers founded the cherry industry in the Pacific States. Among State stations, New York (Geneva) has taken the lead, introducing two new varieties so far. South Dakota has introduced several varieties, and work is in progress at the Iowa and North Dakota stations, the Federal field station at Mandan, N. Dak., and in Canada, where one new variety has been introduced. In

addition, collections of breeding material are maintained in Ohio, Colorado, Utah, California, and Oregon. In the search for necessary characteristics, native American wild cherries are being extensively used in some of this breeding work.

Apricots (probably native to China) are grown commercially only in Pacific Coast States because the blossoming habit of the trees makes them particularly susceptible to spring frosts in the colder regions. The species grown commercially is the common apricot, but several other species and subspecies are useful for breeding, including the black apricot, the Japanese apricot, the Russian apricot, and the Manchurian apricot. The raw material used by breeders consists largely of older varieties from England (Blenheim, Moorpark), from France (Peach, Guillans Early), and from the Union of Soviet Socialist Republics (Alexander, Budd), and newer American strains (Newcastle, Alameda). The chief objectives of breeders are to combine the good characteristics of these varieties and eliminate the faults; and also to develop hardier types adapted to a wider territory. Apricots from northern Asia are particularly hardy, but there is need for still more material of this sort.

Among the wide crosses that have been made is that of the apricot with the plum, producing the so-called plumcot—though some cytologists do not consider this a true hybrid.

Systematic breeding with apricots is quite new. The Department began work at Palo Alto, Calif., in 1922, and about 60 promising hybrids are now being studied and tested. Work began in New York (Geneva) also in 1922, and so far one variety (Geneva) has been named. In 1924 the North Dakota and the South Dakota stations began breeding work; the latter station has been experimenting with material from Manchuria and Siberia. Breeding work in Davis, Calif., began in 1930. Apricot-breeding projects are also in progress in Australia and Morocco.

Citrus Fruits

Grown for thousands of years in the Orient, citrus fruits were established in Florida by 1579 and California by 1769 and were worth over 134 million dollars to growers in the United States in 1934. They are an outstanding source of vitamin C and an important source of vitamin B. Their unique sprightly flavors come from a combination of sugars (sweetness), acids (tartness), glucosides (bitterness), esters (aroma), peel oil (aroma). The chief types, including those used as rootstocks, are sweet orange, sour orange, King orange, tangerine orange, satsuma orange, shaddock, grapefruit, pummelo, citron, lemon, lime, Ichang (lemon), kalpi, calamondin, and kumquat.

Today, large production, decreasing returns, and increased competition place great stress on improvement by breeding. Breeding work was begun in Florida by the Department in 1892 and by the State stations in California in 1910, in Florida in 1924, in Alabama in 1933, and in Texas in 1934. It is being carried on in Hawaii, Mexico, Brazil, Argentina, Spain, Italy, Greece, Morocco, Palestine, Japan, China, India, Zanzibar, Australia, and New Zealand.

Improvement of citrus fruits in the United States prior to the use of modern breeding methods was by introduction of varieties from

abroad, the selection of chance seedlings, and probably selection of some bud mutations. The record of the earlier development of varieties is full of interesting vicissitudes. Among the outstanding successes is the story of the Washington Navel orange. Through the help of a missionary, William Saunders, who was then Superintendent of Gardens and Grounds in Washington, D. C., got 12 navel orange trees from Bahia, Brazil, in 1870. Mrs. Eliza Tibbetts, migrating to Riverside, Calif., in 1873, took two of them along. They proved to be almost as important in California history as the discovery of gold, since all of California's Washington Navel orange plantings came from these two original trees.

The objectives of breeders today include: Tree characters—compactness, vigor, productiveness, disease resistance, cold resistance, congeniality with rootstocks, and correct market maturity. Fruit characters—high dessert quality, seedlessness or near seedlessness, correct size and shape, good shipping and storage quality, attractive exterior, standard vitamin C content, firm pulp for canning, and attractive juice color. There are other special requirements for rootstocks. In the past the chief methods of improvement were by: (1) Selection of superior seedlings without controlled pollination. Citrus fruits have the peculiarity of producing several seedlings from one seed. Usually only one is the product of the union of male and female parental cells; the others are practically buds within the seed tissue and are produced nonsexually. This adds to the difficulty of breeding work. (2) Selection of superior bud mutations. This has been very important since the intensive studies made by A. D. Shamel, of the Department, and his coworkers. In the last 18 years, probably 10 million buds have been sold to California growers alone as a result of this work. (3) Hybridization, especially between different species of citrus. This method is being used chiefly to create new types with unique flavors and other characteristics.

The last two improvement methods are still actively employed.

Hybridization is being carried on by the Department and State stations, with promising results in several cases. Almost every kind of citrus fruit has been crossed with almost every other kind. Among the new types produced are the tangelo (mandarin orange × grapefruit); tangelo × grapefruit; tangerine × sweet orange; Perrine lemon (lemon × lime); citrange (trifoliate orange × sweet orange); citrangequat (citrange × kumquat); citrangedin (citrange × Calamondin); limequat (lime × kumquat); tangemon (mandarin × lemon); tangor (orange × mandarin); orangelo (grapefruit × orange); oramon (lemon × orange); lemelo (grapefruit × lemon); lemon × grapefruit; lemon × citron. The hybrids are so numerous and varied that naming them is becoming a problem in itself.

In connection with breeding work, several technical problems are being studied, especially polyembryony (the asexual production of embryos) and the inheritance of disease resistance.

Subtropical Fruits Other Than Citrus

While many of the subtropical fruits important in other regions, such as the loquat, jujube, cherimoya, granadilla, jaboticaba, and white sapota, are relatively unimportant in the dietary and agri-

culture of the continental United States, others, such as the pineapple, fig, olive, avocado, and date, are the basis of established industries; and still a third group, including the mango, papaya, lychee, and guava, give promise of taking rank with those already firmly established. Most of those in the first group are adapted to one section or another of the United States, or to Hawaii, the Philippines, Puerto Rico, and the Canal Zone. With practically all of these fruits, breeding work and genetic studies are only at their beginning in this country, though there are some extensive and valuable collections of germ plasm made by such farsighted plant explorers as David Fairchild and Wilson Popenoe and their coworkers. Though the areas of possible cultivation are limited, interest in several of the subtropical fruits is growing, and with it the need for superior forms achieved through breeding. The raw material is fascinating in range and variety, and breeders are sufficiently well acquainted with it to have worked out techniques and determined the desirable objectives in considerable detail.

Fig growing is now the basis of a sizeable industry in California and Texas. Smyrna fig culture in California did not get into its stride until the discovery, at the end of the last century, that a small wasp, which makes its home in the inedible caprifig, is necessary for the pollination of quite a different type, the Smyrna fig of commerce. Improvement of figs—as of most other subtropical fruits—since that time has been largely by introductions from abroad and the selection of superior strains. However, hybridization has been conducted in California since 1922, and of some 4,000 hybrid seedlings that have fruited, several have been found with desirable characteristics. In Texas, hybridizing was started in 1935.

Avocado breeding is in the fortunate position of having a rich collection of varieties brought in by Wilson Popenoe and some of the early pioneers, available for hybridizing to obtain combinations of resistance to low temperatures, high quality, long range in marketing season, and other superior characteristics. These varieties are being intensively studied and several worth-while selections have been made. Although hybridizing has only begun, some excellent hybrids have already been secured and the future looks promising.

Thousands of date offshoots have been brought into the United States by the Department of Agriculture and others, totalling over 140 varieties, and of these some 16 varieties are now important in Arizona and California and many varieties are under test in Texas. Date breeding is an extremely slow process. Methods of controlled pollination have now been worked out, but progress so far has been by mass selection.

Pineapple growing has been revived in Florida since 1933; it is extensive in Hawaii, and fairly extensive in Cuba and Puerto Rico. Hybridization has been begun by the Department; some work is being done in the Philippines; but most of the breeding work is in Hawaii, where promising results are being secured.

The papaya, a "tree melon", is counted an outstandingly fine fruit by those familiar with the best varieties. Florida seems best adapted to papaya culture in the United States, though the fruit is grown in California and Texas also. It is very important in the dietary in Hawaii, the Canal Zone, and the Philippines. The Department has

introduced many strains and related species, and a breeding project is now in progress. Breeding work is also being done in Hawaii, the Philippines, and the Union of South Africa.

The mango, one of the oldest of cultivated fruits, with a flavor somewhat like pineapple and apricot combined, is grown in Florida—where over 200 introductions have been made by the Department, including more than 50 varieties and a number of related species—as well as in the island possessions of the United States. No method of controlled pollination has been worked out, but selection of superior seedlings holds considerable promise, and it is now being practiced in breeding for disease resistance and other characteristics.

Miscellaneous subtropical fruits with which little breeding work has as yet been done in this country include the olive, persimmon, granadilla, guava, feijoa, jaboticaba, pomegranate, jujube, lychee, loquat, white sapote, and cherimoya. All have possibilities for improvement and some are exceptionally interesting.

Nuts

Until recent years there was practically no attempt to develop better nut trees by controlled breeding. Nature's products usually seemed quite good enough. There is not much breeding work under controlled conditions today, but it has been started, and though the work has many difficulties, it also has very great possibilities for those with the inclination, the time, and the facilities to carry it on.

Chestnut breeding became a pressing need because the American chestnut, a magnificent tree characteristic of large forest areas in the eastern United States, was practically killed out by chestnut blight, a disease from the Orient that first appeared on Long Island, N. Y., in 1904. Some hybridization of American and European chestnuts had been done before the blight appeared, but the hybrids were doomed because both parental species are highly susceptible. The Japanese chestnut tree is quite resistant, but the nuts lack flavor. Much more promising is the Chinese chestnut (first extensively introduced into the United States in 1907), which is highly resistant to blight and produces a nut as large as the European and often as fine in quality as the American. Present selection and hybridization work, therefore, is practically confined to the Chinese chestnut, with consideration being given to the Japanese. The Department and the Illinois station are engaged in this work, as are several private breeders. No variaties have been officially released by public institutions as yet. Chestnut blight will quite probably be overcome by breeding and it is not impossible that another major enemy, the chestnut weevil, will also be overcome.

Commercial filbert growing is confined to a region in the Pacific Northwest, particularly the Willamette Valley of Oregon and parts of western Washington naturally adapted to the superior filbert varieties of two European species (Barcelona, Du Chilly, Daviana, White Aveline are well known horticultural varieties of these). In the eastern United States these European filberts are handicapped by a fatal blight, which spreads to them from the American species, and by lack of winter hardiness. A few somewhat superior American varieties (Rush, Littlepage, Winkler) are available for growing in the East, but

the breeding problem here is one of developing hybrids with resistance to disease and cold. In the Pacific Northwest, the problem is to develop filberts commercially and culturally superior to those now grown. There is a good supply of breeding material, and work is being actively carried on by the Department (at Beltsville, Md., and Corvallis, Oreg.), the Minnesota station, and the New York station at Geneva, as well as by several private breeders.

The breeding of pecans, the most important nut of the hickory group, is somewhat confused by existing uncertainties as to the sizes of nuts wanted by the market. The shelled-nut market wants very small pecans, and there is doubt as to whether they can be grown profitably except in uncultivated forest groves. The one-time demand for very large pecans has steadily diminished, so that breeding for extra size no longer seems desirable. In addition, most of the best of the older varieties of pecans proved to have so many drawbacks that the nuts are no longer marketed by varieties (as are apples and pears), but the varieties are blended. Nevertheless, selection and hybridization proceeds with certain definite objectives—hardiness (for northern pecans), disease resistance, fruitfulness, size of nut (at present a compromise), shell thinness, shelling quality, kernel quality. The work of the Department is divided regionally; the Illinois Station is carrying on a selection project; several private breeders are active; and pecan breeding by selection is being conducted in New South Wales and in Mexico.

Hickories other than pecans have received very little attention from breeders—the market demand is too limited. Nature has accomplished considerable hybridization between the various species (pecan, shagbark, shellbark, bitternut), and trees of some hybrid forms are available commercially. Hickories superior in thinness of shell, cracking quality, and flavor would fill a real need. A limited amount of selection work is being done by the Department of Agriculture, the stations in Illinois, Ohio, and New York (Geneva), and private breeders.

Breeding the Persian walnut (called English walnut because it first came to this country from England) has largely been confined to selection, which has about reached its limit of practicability. The next step is hybridization to develop varieties resistant to blight and possessing greater fruitfulness, superior hardiness, better cracking quality, and superior flavor. Such work is being conducted by the Department, the Minnesota and New York (Geneva) stations, and at least one private breeder. Selective breeding is being done in Mexico.

Selective breeding with the eastern black walnut is being conducted by the Department, the Illinois, the Minnesota, the Ohio, and the New York stations, and many private breeders. Similar work with the Japanese walnut (much like the butternut) is being conducted by the Connecticut station and several private breeders. The Department is now starting a project to create a form of walnut unlike any now existing by crossing the Persian walnut with the butternut for hardiness and flavor, then with the eastern black walnut and the Japanese walnut for sturdiness and fruitfulness of tree.

Almond breeding is being systematically carried on by the Department in cooperation with the California station at Davis, with the

objective of combining in a few new and definitely superior varieties as many as possible of the superior characteristics of the existing varieties. If this is successfully done, American almonds should not only dominate the American market but have a place in foreign trade. Practically no breeding work has been done with the pistache nut (adapted to hot, dry regions), though it deserves attention. The tung tree, the nuts of which furnish a valuable oil that dries more rapidly and is more resistant to water than linseed oil, was introduced into this country from China by the Department of Agriculture in 1905. The Florida Station began hybridization work in 1929, and the Georgia Station began selective breeding in 1933.

Very little genetic analysis has been made with nut trees, but a good deal of valuable technical work has been done on pollination technique, pollen viability, receptivity of the stigma, fertilization, and incompatibility.

Flowers

The enormous number of our named varieties of flowers has resulted from generations of breeding effort on the part not only of commercial growers but of untold numbers of amateurs from every walk of life. There are 15,000 varieties of roses alone, 8,000 varieties of tulips, 7,000 varieties of dahlias, 7,000 varieties of narcissus. Many of these are romantic in origin and testify to the deep love of the breeder for his work.

Yet most of this work has been unscientific in nature, and too much of it still is. Flower breeders, both amateur and professional, have on the whole had only a slight acquaintance with the modern science of genetics, which has played so important a part in the breeding of the more important food crop plants. They proceed by trial-and-error methods and wait for the breaks, and the result is much waste of time and effort, and the persistence of practices that cannot bring the expected results. Modern genetics goes out and makes the breaks. The time has come when those interested in breeding flowers should go to some trouble to study the facts and theories of heredity developed since Mendel's paper was rediscovered in 1900, and to master the technical methods that have revolutionized other fields of plant breeding. Genetics has a vast amount to contribute to the improvement of flowers, though professional geneticists have paid relatively little attention to ornamental plants except as these have been used as laboratory material for the study of theory.

Flowers differ in their requirements for pollination, depending on the structure of the flower parts and on different degrees of self- and cross-sterility. Emasculation (removal of the anthers) is quite commonly necessary in cross-pollination, and the bagging technique must frequently be used to prevent contamination with unwanted pollen. The older method of improvement was by selecting superior plants from a large mixed mass; it is still widely used, but it is slow and very limited compared with later methods. Then came line breeding, or selection from the progeny of a single plant. Hybridization, the most important method in plant breeding today, will probably be used more and more with flowers; but what some flower breeders fail to realize is the necessity for continuing the breeding work after the first hybrid generation, to provide segregating groups with different com-

binations of parental characteristics; and also the necessity for keeping the right kind of records. Unusual plants produced by gene mutations or by variations in the number, structure, or behavior of chromosomes are sources of valuable material, and some of the newer methods of artificially bringing about these changes seem promising for the flower breeder. This emphasizes the need for an understanding of chromosomes, which has contributed definite practical results—notably, for example, in the case of double-flowered stocks—and will contribute much more.

Representative flowers considered are the amaryllis, China-aster, canna, carnation, chrysanthemum, dahlia, gladiolus, hemerocallis, iris, lily, nasturtium, rose, snapdragon, double-flowered stock, and sweet pea. Some of these have a rich historical background and several have been subjects for much patient selection and hybridization. In two cases—the China-aster and the snapdragon—breeding has been responsible for the development of forms resistant to destructive diseases. In all cases there are as yet untouched opportunities for improvement through better breeding methods, a closer study of inheritance and cytology, or the use of germ plasm not yet incorporated into our cultivated varieties.

Miscellaneous Forage and Cover Crop Legumes

Among the Cinderellas of the plant world are many humble legumes—relatives of our common peas, beans, alfalfa, and clover—that are valuable for soil building and conservation because they will thrive where better-known crops fail, and they enrich the soil with nitrogen. Some are known as weeds; some have been grown by farmers here and in other countries both for forage and for human food. Not much has been done to study the adaptability of these plants to special conditions or to explore the possibility of improving them by breeding; but as this country passes out of the large spending stage in agriculture, they will be given more attention. Their use is like having a savings account in the bank.

A few of these plants are already of considerable value. The cowpea is extensively grown, a large number of varieties are recognized, and some State stations as well as the Department have carried on breeding work with it. At least one outstanding variety, the Victor—resistant to wilt and nematodes—has been developed by controlled hybridization, and others have resulted from selection. The field pea, also widely used, has given good results with selection and is now the subject of breeding programs by the Department and by the Georgia, the Alabama, and the Tennessee stations. The velvetbean is a leading legume crop in the Southeast; several superior varieties have resulted from selection over a period of years, and a breeding program with this crop would probably be profitable. A large number of species of vetch are in general use, and the Oregon station, cooperating with the Department, has led in developing improved varieties. The lespedezas or bush clovers, invaluable in southern agriculture, have recently been receiving considerable attention. New varieties have been introduced from Japan and Manchuria, and the Department has been carrying on active selection work, but the possibilities are by no means exhausted as yet. The bur-clovers are grown to

some extent and have received some attention from breeders, but the species has rich possibilities not yet explored. Rattlebox (crotalaria) is a new forage plant in the United States, and the Department, cooperating with the North Carolina, South Carolina, Georgia, and Florida stations, has been selecting early varieties. Kudzu and the peanut are grown as forage crops, but no breeding work has been done with them from this standpoint.

Among the completely or almost completely neglected legumes, some of which undoubtedly have potential value in the United States, are the milk vetches for arid conditions; beggarweed or tick trefoil; bonavist, long grown in Africa and Asia; the chickpea; fenugreek, grown to some extent in California; the grass pea and guar, both used in India for animal and human food; kidneyvetch, the subject of breeding programs in Wales and Denmark; *Lotus*, commercially important in Europe and Australia; lupine, now being bred by German and Russian workers; the pigeonpea, a valuable legume in tropical countries; sainfoin, long grown in Europe; serradella, used in Europe on acid sandy soils; *Sesbania*, adapted to wet soils in the South; sulla, used in Europe and Australia.

Interesting technical studies with some of these plants, both in the United States and abroad, have helped to develop fundamental facts useful in breeding.

Miscellaneous Grasses

Man lives largely on grass. His grains are grasses. His meat and milk are transformed grass; in the United States, grazing lands furnish nearly half the sustenance of livestock. In addition, grasses are of great importance in reducing erosion and maintaining soil fertility; and this country spends over $100,000,000 a year on private lawns, and some $90,000,000 on turf for other purposes. Systematic efforts to improve grasses by breeding are therefore of major importance. In the United States these efforts with the miscellaneous grasses are relatively new; many State projects were begun not more than 5 years ago -though sporadic work has been going on for a long time—and it is too early to expect results. The work is older in Canada, the British Isles, New Zealand, Australia, Sweden, Germany, Denmark; and probably more has been accomplished at Aberystwyth, Wales, than anywhere else. But modern genetics proves that plants must be bred for specific environments. We shall have to solve our own grass-breeding problems.

The sources of breeding material are as wide as the world, for each region, from desert to swamp, from the Arctic to the Equator, from mountain to sea beach, has its peculiar grasses, adapted to persist and thrive there. The number of grasses developed under these varied conditions is extremely large and the range in characteristics correspondingly great. Long ago the migration of grasses to other regions began. South American cattle live on forage grasses that originated in tropical Africa, cattle in the Corn Belt on grasses from Europe. The United States today may be divided into six regions from the standpoint of climate, and the major types of grasses in these regions into nine broad groups—Kentucky bluegrass, Canada bluegrass, and timothy; the redtop and bentgrasses; orchard grass and

tall oatgrass; Bermuda, Johnson, and Dallis grasses; carpet, Napier, Bahia, and Para grasses; awnless bromegrass and crested wheatgrass; native short grasses and prairie grasses; slender and western wheatgrasses; Sudan, reed canary, and other grasses.

What are the needs and possibilities for improvement by breeding? Shy seed production handicaps the use of many valuable grasses. Diseases play havoc in certain regions and with certain types. Some excellent grasses are not aggressive enough in growth to maintain themselves in competition with other plants; others are too aggressive to make possible the maintenance of desirable legumes in mixture. Some are not vigorous enough in renewing growth after grazing or cutting. For some pasture and range uses increased longevity is needed, and this may be largely affected by drought resistance and winter hardiness. Greater ability to thrive in wet and in saline soils is very important in some places. Some good grasses would be more useful if they were more palatable to livestock and had higher nutritive value. In turf grasses, texture, ability to withstand hard usage, and uniformity are of major importance. On all of these eight counts there are sufficient variations within the best-adapted types to give promise that breeding by selection or hybridization would accomplish improvements. Already, selective breeding work in the United States has furnished improved new strains, either introduced or soon to be ready for introduction, of Washington and Metropolitan bent, velvet bent, highland reed canary grass, tall fescue, tall oatgrass, Bahia grass, tift Bermuda grass; and in Canada, of slender wheatgrass, crested wheatgrass, bromegrass, and orchard grass. Twenty-three additional improved strains in Canada are being increased for more extended trials and distribution.

The manipulations in grass pollination by controlled methods are often as fine as jeweler's work and must be performed under a magnifier or microscope. Ingenious techniques have been developed, and much study has been given to flowering habits, to the question of self sterility, and to chromosome behavior, especially in wide crosses. There has been little work as yet on the mode of inheritance of characteristics.

Timothy

Timothy, the most important of the agricultural grasses, was first cultivated in North America, though it is of European origin. It received its present name, presumably, from Timothy Hansen, who introduced it into Maryland from New England or New York about 1720. In 1929, one-third of the total acreage in hay in the United States was all or part timothy. It is also widely used in pastures, being one of the most palatable pasture grasses to livestock.

Varieties and strains of timothy differ rather widely in earliness or lateness of maturity, length and degree of fineness of stems, width of leaves, tendency for the leaves to remain green, resistance to the principal timothy disease (rust), and in other ways. These variations are the basis for breeding improved kinds. The objectives of breeding programs include rust resistance, increased productivity, early varieties for the South, late varieties for the North, varieties adapted for hay production when grown in mixtures with clover or alfalfa, and varieties especially suitable for use in pastures.

Timothy is normally cross-pollinated, so that most of it is quite hybrid in make-up. Methods of breeding include repeated selection among open-pollinated strains, and also some self-pollination and crossing of inbred lines.

Up to the end of the last century, timothy was timothy; there were no improved varieties, as there were of wheat, oats, and other grains. In 1889, Willet M. Hays pioneered in making selections of timothy plants at the University of Minnesota, for increased productivity and a longer harvesting season. In 1894, A. T. Hopkins, a well-known entomologist, began making selections and continued the work for several years. Hopkins had a notable faculty for arousing enthusiasm in others over the possibilities in timothy improvement.

After 1900, timothy breeding was started at Cornell University and is still being carried on there. An early and a late variety, both somewhat rust-resistant, have been produced, and a number of technical studies have been completed. Other stations that have had timothy breeding programs include those in Iowa, Minnesota, Pennsylvania, Kentucky, New Jersey, and Wisconsin. Some breeding work was conducted by the Department from 1899 to 1909, and thereafter it was carried on more intensively in cooperation with the Ohio Station. The outstanding variety developed from this work is the Huron— late, leafy, rust-resistant—released in 1933.

Abroad, several varieties with regional adaptation have been developed at Svalof, Sweden, and at the Welsh Plant Breeding Institute, Aberystwyth, Wales. Notable among Welsh developments were low-growing types that root at the nodes, especially suitable for pasture. These have been tried only to a very limited extent in the United States. Timothy-breeding work has also been carried on in other European countries.

Technical studies with timothy include biometrical analyses of yield trials, determinations of chromosome numbers, seed production under self-pollination, self-sterility, and effects of selfing on vigor, yield, disease resistance, and other characteristics.

Alfalfa

Alfalfa, which means "best fodder" in Arabic, is very old. One writer has suggested that it was the "grass" on which Nebuchadnezzar fed when he was driven into the fields. It was fed to sleek chariot horses in ancient Rome. The Spanish conquerors of Mexico and Peru took the Indians' gold but brought them alfalfa seed. Forty-niners, sailing to California around the Horn, picked up some Chilean alfalfa and took it with them. It soon spread to other Western States.

It did not winter well in the North. But in 1857 Wendelin Grimm, a German immigrant, brought alfalfa from his homeland into Minnesota. For 50 years he stubbornly and patiently saved seed from plants that survived the winter. In the end, he had the one hardy alfalfa. Subsequently, experiment station workers made Grimm alfalfa famous.

This was both a boon and a drawback. Grimm alfalfa was so satisfactory that there was little incentive to develop other improved varieties. Nevertheless, between 1903 and 1915 a number of State and Federal workers were busy breeding alfalfa, and they did some

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interesting work introducing varieties that are now standard—though the limitations of the methods they used were not then fully understood. This work was stopped by the World War, with its emphasis on food crops rather than feed crops.

Some years later, stands of Grimm and other alfalfas began to die out prematurely and alarmingly, first in Iowa, Kansas, and Nebraska, then in other Midwestern States. By 1925, Federal workers traced the mysterious destruction to the organism now known as the insidious phytomonas—*Phytomonas insidiosa.* Today it costs farmers several million dollars a year in lost alfalfa crops and expense of reseeding. This catastrophe put pressure on breeders to see what they could do.

Plant explorers of the Department have scoured the earth for alfalfas, bringing back a thousand different strains. None proved to be very resistant to the disease except some from Russian Turkistan, northern India, western China, northeastern Iran. The chief problem in the present breeding program, then, is to combine the resistance of these strains with the good commercial qualities found in Grimm and other American alfalfas. Dovetailing with this is another problem of developing strains especially well adapted to various broad regions in the United States. Other desirable objectives include heavier seeding, better forage quality, suitability for grazing, insect resistance, drought resistance, and higher protein content.

For a concerted attack on these problems, State and Federal breeders have recently organized the Alfalfa Improvement Conference, to insure close cooperation between all the workers concerned.

Work has been done on breeding technique; correlations between various characteristics in alfalfa; hybrid vigor; inbreeding and its effects; the possibility of making species crosses; and segregating and purifying strains for disease resistance and cold resistance, with the object of recombining them. The general genetic behavior of alfalfa has been explored, but little has been done on the inheritance of specific characters. Recently a number of workers have been interested in the cytological study of the plant.

Soybeans

In the Orient soybeans have been grown since time immemorial, and it has been said that some oriental countries could not exist without them. The plant was introduced into the United States (Pennsylvania) as early as 1804. Since 1890 most of the State stations have experimented with it, but it aroused comparatively little enthusiasm until the last few years. In that time its rise has been dramatic. Acreage has increased 110 times in 28 years, seed production 13 times in 15 years. The United States is now second in seed production to Manchuria, though still far behind that "Land of Beans."

The reason for this phenomenon is to be found in the versatility of the soybean. Every part of the plant is useful, and a tabulated list of uses takes up a page of fine print. Forty-five oil mills in the United States are now crushing soybeans; 40 concerns are manufacturing soybean food products; 75 factories are turning out industrial products made from soybeans.

Altogether, the Department of Agriculture and State stations have brought in some 10,000 selections for testing and experiment. Thirty-two stations and the Department are engaged in breeding work. About 100 varieties have been introduced for commercial growing since 1894. Yet the breeding work is only at its beginning, for several reasons.

The soybean is very particular in its local requirements. This means that special varieties for each kind of use have to be developed for each separate region or locality. This has long been done in the Orient. The uses themselves demand quite distinct characteristics. Thus beans grown for oil should have a high oil content and a high iodine number, which is associated with good drying quality. The lecithin content of the oil is also important for some industrial uses. Beans for certain industrial uses should have a high protein content. Beans grown for food protein should be high in the three amino acids, cystine, tryptophane, and tyrosine. Those grown to be cooked as dried whole beans should be tender and of excellent flavor. Those grown for use as green shelled beans must be especially adapted to this purpose. And so on.

Progress has been made in developing varieties for local use that meet these needs. But there is much still to be done. The breeder, however, has a wealth of material, and the measurements and tests already made indicate the range of some of the characteristics among different varieties. Oil content, for example, ranges from 12 to 26 percent, iodine number from 118 to 141, protein content from 28 to 56, lecithin content of the oil from 1½ to 3 percent; the percentage of the amino acids mentioned varies over a wide range. The breeder can choose and combine, build up this, reduce that. Diseases are not yet a serious factor with soybeans in this country, but it is known that resistance to several diseases varies also, and when that complication enters he has some information on which to proceed.

The soybean is a self-fertilized plant, and artificial crossing is difficult and tedious. Hybridization, however, offers the best means of combining desirable characteristics and getting a wide variety of segregates from which to make selections. The inheritance of a good many characteristics of the flower, stem, leaf, and seed has been worked out, and a beginning at least has been made in mapping the location of a few genes on the chromosomes.

Clover

The ancient belief that clover brings luck has proved to be abundantly true for agriculture. First grown as a cultivated crop in the sixteenth century, its use became the foundation for good farming practice. It is at once food for the land and food for animals. Systematic improvement by breeding, a recent development, is being carried on in several countries.

Natural adaptation has been the prime factor in developing regional strains of red clover—the most important of the clovers in the United States—that differ in productivity, winter hardiness, and disease resistance. For several years, these regional strains have been closely studied by the Department in cooperation with the Kentucky, Ohio, and Iowa stations, partly to determine regional needs, partly to dis-

cover superior plants that may be used in breeding. Broadly, the chief objectives for the three red-clover regions of the humid eastern United States are: Southern—disease resistance, especially to anthracnose; central—disease resistance and winter hardiness; northern—ability to withstand a long period of winter dormancy. In addition, powdery mildew, the potato leafhopper, and the clover root borer are clover enemies in all regions.

So far, anthracnose-resistant strains have been developed by the Tennessee and Kentucky stations, and the Department of Agriculture has during recent years cooperated in improvement of the strains developed by the Tennessee station many years ago. Lines resistant to powdery mildew have been developed in cooperation with the station in Wisconsin. Other developments are in progress in cooperation with the Illinois Station; and the stations in Minnesota, Pennsylvania, Tennessee, Indiana, New Jersey, and Idaho have red clover breeding programs under way. Abroad, nearly all European countries, and Australia and New Zealand, are doing breeding work with red clover, and in several of these countries superior strains have been introduced. Selection from natural stocks has played a large part in improvement programs, but the isolation of self-fertile lines and controlled crossing are also used. The Welsh Plant Breeding station has carried on important basic studies.

There has been no breeding work with white clover in the United States, but work has been done in New Zealand, Denmark, Sweden, Finland, and Wales. Crimson, alsike, subterranean, berseem, and Persian clovers have not been bred in this country, though some of them have received attention abroad.

Sweetclover, which was classed as a weed a few years ago, has had a phenomenal rise in popularity and now holds an honorable place in the agriculture of the north-central region and the Great Plains States, as well as in several foreign countries. Several varieties, resulting from selection and introduction from abroad, have been introduced by the Department of Agriculture, by several State stations, and by individuals. Canada leads in systematic breeding, and work is also in progress in Wisconsin, Minnesota, Kansas, Washington, Texas, Nebraska, Illinois, West Virginia, and Idaho, as well as in the Union of Soviet Socialist Republics and in Germany. One of the chief objects in all breeding studies is the development of strains low in coumarin, since the presence of coumarin or of closely related substances appears to make spoiled sweetclover hay toxic to livestock and lowers the palatability of the green plant. So far, the results in this direction are promising.

Studies have been made of fertility and sterility relationships in clover that have cleared up misconceptions, and pollination techniques have been developed. There have been some cytological investigations and genetic analyses, especially in sweetclover.

Hops

Beer is made with hops, water, malted barley and other cereals. The hops supply lupulin (resins and essential oils) which gives the beer its characteristic flavor, and tannins which help to clear it. Thus hop growing is vital to the brewing industry, though unfortunately for

growers, a small quantity of hops makes a great deal of beer. In Europe hop growing goes back at least to 768 A. D. Kings who liked hopped beer sometimes compelled farmers to grow hops by law; those who preferred beer without hops forbade farmers to grow them. Kings of the latter type were apparently in the minority, and in Europe much effort was devoted to improving hop varieties.

The hop is a peculiar species. It is a perennial vine, grown on poles or trellises, and extremely sensitive to sun, wind, heat, rain, insects, and diseases. Male and female flowers are borne on separate plants, though it is not unknown for a plant to change its sex, sometimes more than once. The hop of commerce is something like a fir cone but more papery and fragile, and it is borne only on the female plant. Fertilization is not necessary for the development of the hop, but the cone bears seeds only when the flowers are fertilized.

Commercially hop vines are repoduced by cuttings, like sugarcane and some other plants. Since the seed is always a product of cross-fertilization, the plants are of hybrid origin genetically, and seeds from the same mother will produce many different types. It is chiefly from these diverse seedlings that hop breeders get their raw material for superior selections. Hop breeding presents some especially knotty problems and has some difficulties similar to those of animal breeding. Because the male plant bears no cones, it is uncertain just what it contributes to improvement, even when controlled pollination is practised so that the nature of the male parent is known.

Breeding work in the United States is relatively new. It was started by the Department of Agriculture in 1900, but later the World War discouraged and prohibition finished it. Now, however, it is being continued again in cooperation with the Oregon station. The chief objectives are increased yield; favorable periods of maturity; resistance to several diseases, especially downy mildew, the bane of growers in various sections; and quality, an elusive character depending on type, color, soundness, and lupulin content. Of these, only the amount and quality of lupulin can be accurately measured by laboratory methods. The importance of quality may be better understood from the fact that at present brewers in this country frequently mix some European hops with their American-grown hops and usually pay a high premium for hops from Germany and Bohemia.

Thus far the breeding program in the United States has been concerned largely with making a close study of the available raw material so that an accurate catalog of plant characteristics may be available. It has been necessary to work out techniques for some of the more difficult problems such as control of pollination, evaluation of breeding methods, controlled development of the downy mildew disease, measurement of resistance, and determination of quality. With these difficulties on the way to solution, a basis is being laid for future breeding work. Good results with seedling selection in Europe indicate the possibilities, though improved European varieties have failed to give comparably good results in this country. Growers on the Pacific coast are now very much interested in hop improvement by breeding, and the New York (Geneva) station has also recently initiated a varietal improvement project.

Forest Trees

In forestry, genetics is almost a new word, and breeding as it is practiced with other economic plants is a virgin field. Economic pressure in the wood-using industries and the urgent national need to build up forest areas, however, have turned attention to tree breeding as a vital part of an intelligent forest program. There is ample evidence that, like other plants, forest trees differ individually in the characteristics that are of value to man; and the possibility of breeding superior individuals and populating large areas with their descendants, as is done with wheat and other crops, is one we cannot escape exploring.

Obviously there are difficulties not involved with small, quick-maturing plants, in many of which pollination is fairly easily controlled, and it will take a good deal of study and ingenuity to overcome some of these difficulties. The methods and possibilities, however, are fundamentally the same as with other plants. They include a clear formulation of the type of tree desired for a given use; the selection of superior individuals by extensive testing and observation; establishing pure lines where possible; as much use of vegetative propagation, by cuttings, etc., as possible, to reproduce superior individuals absolutely true to type; the crossing of strains, varieties, species, and genera, both to creat new types and to obtain hybrid vigor; a thorough study of polyploids—that is, individuals with an increased number of chromosomes in the cells beyond the normal number—as sources of especially valuable stock. At present, polyploids are receiving special attention because these plants with extra chromosomes are so often characterized by unusual size and vigor, but the enlarged cell size in some types of polyploids, resulting in coarseness of structure, may prove to be a drawback for many commercial uses.

It need hardly be said that research in the cytology of forest trees, particularly in cytogenetics, and in the mode of inheritance of characteristics, should be carried on along with a practical program. Much work is also needed to determine standards and tests applicable in the forest and in the selection nursery.

In every one of these fields, a beginning at least has been made. Fairly extensive tests are being conducted to determine superior varieties and individuals for both regional forest requirements and use requirements, and these tests include disease resistance, weather resistance, rapidity of growth, and other important characteristics. Hybrids, superior in various ways to either parent, have been made, a notable example being the creation of fast-growing poplar hybrids for paper pulp. Experiments are being carried on in methods of controlled pollination and vegetative propagation. Efforts are being made to devise better progeny tests—not an easy matter under practical forest conditions—and ways to reduce the time involved in testing. Perhaps the least work is being done in fundamental research in genetics; but so far there are very few geneticists in forestry—practically none in comparison with other branches of agriculture.

To other plant breeders the amount of breeding work in forestry would seem small indeed, and doubtless quite elementary in nature. Nevertheless, the foundations necessary for a science of forest genetics

are being laid, in the United States and in other countries. Moreover, the forest-tree breeder, challenged as he is by difficulties, is in the stage where he is filled with enthusiasm for the possibilities not only of eliminating some of the most costly mistakes of past forestry practice, but of adding something genuinely valuable to nature's own magnificent achievements in creating trees useful to man.

Angora Goats

The goat performs two useful functions. It cleans up brush, thereby saving its owner a great deal of work; and through its digestive processes, it converts the brush into food and clothing for man, in the form of milk, meat, mohair, and skins.

The domestic goat is probably descended from the pasang or Greek ibex of the Near East. The long-haired Angora was originally developed by the Turks centuries ago. The first importations to Europe were apparently made in the sixteenth century, and to the United States as late as 1849. South Africa, Turkey, and the United States are the leading producers today. There are now over 3 million Angoras in this country, and the industry is concentrated chiefly in the Southwest, with Texas well in the lead. Of the 15 million pounds of mohair produced in the six leading States in 1935, Texas produced 13 million.

Improvement of the Angora goat has been entirely in the hands of private breeders. In the range herds, it has been carried on by the method of breeding high-grade does to registered bucks that conform to the standards of the breed association. Very little research work on breeding or genetics has been done by public institutions. The Texas station has been the leader in this field, and at its branch station near Sonora it is now carrying on three active projects on inheritance of type, inheritance of cryptorchidism or undescended testicles, and cytological and hybridization studies.

The best present representatives of the breed produce up to 75 percent more mohair than the average for the country. But there is a very great lack of uniformity even in good herds. If further progress is to be made, a research program will be needed to work out better methods than those now in use to determine an animal's inheritance, and a far better knowledge of the mode of inheritance of characters concerned in the production of good fleeces. Research usually pays well, but there are many difficulties and complications involved in such a program, and it can only be carried on with the active encouragement of the industry.

Meanwhile certain practical steps might be taken by the industry that would tend in the right direction. Among these would be a system of pedigree recording based on production of mohair, with certification of the records, as with dairy cattle and poultry; the selling of mohair on a quality rather than a weight basis, to stimulate improvement of the breed from this standpoint; and the adoption of different methods of awarding prizes at shows, on the basis of get of sires and outstanding families rather than individual appearance—a practice that would be in line with the use of the progeny test, which is overwhelmingly important in evaluating breeding stock, whether plant or animal.

Milk Goats

The milk goat is a handy pocket edition of the cow, and it will subsist where the keeping of cows is impracticable. In certain areas and under certain economic conditions, it can be an important factor in contributing to the family food supply. The milk is not significantly different from cows' milk in nutritive value, and goat meat is palatable and wholesome. The official maximum production record in the United States, made by a Saanen doe, is nearly 7 quarts a day for a period of 9 months and 10 days. Average production is very much under this, and there is great variability between individuals.

Efforts to improve the productivity of milk goats in the United States, therefore, are worth while not only from the standpoint of the present industry, with its breeding and dairy investment, but also as one method of economically raising the nutritional level of some sections of the population.

In this country, only two projects have been carried on by public agencies involving research and experiment in milk goat breeding—one conducted by the Department, one by the New Mexico station.

The Federal project was started in 1909. It has consisted largely in grading up common American does by crossing and top-crossing with registered Saanen and Toggenburg bucks. Progress has been slow partly because of the very small number of breeding does used. However, the average length of the lactation period has been increased 145 percent over that of the native does, and the average annual milk yield by 335 percent. Analysis shows that the period of maximum production is between 4 and 6 years of age. Index measurements of the sires used show marked differences in ability to transmit superior inheritance to daughters.

At the New Mexico station, native does have been graded up by the use of registered Toggenburg bucks, and studies have been made of the inheritance of horns and wattles, length of gestation, prolificacy, sex ratio, and the effects of inbreeding and outcrossing on milk production and birth weight of kids. Marked increases in production were obtained from the top-cross does, and several does in the herd have made creditable records under advanced registry. Line breeding was practiced with three outstanding bucks, the results indicating that it would be worth while to continue this as an experimental procedure. Fertility in the herd was high, 144 parturitions producing 286 kids.

Other researches with milk goats include nutritional experiments with the milk and studies on the physiology of milk secretion, including the effect of pituitary extract on lactation. There has also been a limited amount of genetic research on inheritance of horns, wattles, short ears, color, cryptorchidism, multiple births, and a peculiar nervous instability.

Improvement of herds has been mainly in the hands of private breeders and their three registry associations. Considerable progress has been made, but more might be done by the keeping of more complete records; the development of a more extensive record-of-performance program; the more extensive use of proved sires through a system of exchanges; the elimination of factional tendencies among

groups of breeders; and the working out of better procedures for the selection of breeding animals. There is a need also for further research and experiment on the uses of goat products, and for more study of the economics of production.

Dogs

Dogs supplement the brains of men. Their usefulness depends almost entirely on intelligence and temperament. No other animal serves so many purposes; they are hunters, guards, companions, guides, messengers, herders, detectives, haulers and carriers, scavengers, and even, in parts of the world, sources of fur and food. It is surprising, then, that so little has been done in the way of systematic research in the genetics of the dog, in spite of the fact that in other fields--physiology, psychology, medicine--work with dogs has helped to make possible some major scientific advances of great benefit to humanity.

Scattered studies have furnished information on the inheritance of coat colors, which apparently depend on many genes, often with multiple effects. Certain characteristics of form and structure have also been studied, including the inheritance of modified secretion of the endocrine glands, which has been under investigation by Stockard at the Cornell University Medical College. Some work has been done on the inheritance of aptitudes, notably at Fortunate Fields, in Switzerland, where German Shepherd dogs have been trained as guides for the blind and for army and police service. Here marked progress has been made in breeding superior animals by assuming that valuable characteristics were controlled by a few major genes.

In practical breeding, dog competitions of various kinds have had a marked influence, since persistent winners at field trials and dog shows have a favored position as breeding stock. On the whole, this has probably been a good influence in dog breeding, though from the standpoint of sound scientific practice undue weight is given to the appearance or performance of the individual animal. Awarding prizes and selecting breeders on the basis of a genuine progeny test would put dog breeding on a sounder genetic foundation.

In some cases these contests have been responsible for splitting a breed in two different directions, one strain being especially adapted to perform well in the field, the other being notable for show points. The field competitions greyhound racing, dog-sled racing, hunting and retrieving contests, sheep-herding contests, obedience trials—are of interest as indicating certain kinds of measurements that would have to be developed in a program of genetic research so that one dog might be accurately compared with another.

What are the possibilities in genetic research for the future? There is little doubt that it would help to accomplish improvements in dogs themselves, especially in the development of types for special purposes. Beyond this, however, is the fact that dogs are probably better suited than any other animal for investigations in the inheritance of psychological traits. These traits are important in many farm animals; nothing is known about their behavior in heredity. The Department of Agriculture has recently made a modest beginning in an investigation of this sort, using the Puli dog—a sheep dog of

Hungary—which is being crossed with various other breeds. From these experiments it is hoped that worth-while information may be developed regarding the inheritance of intelligence and certain aptitudes of practical value in dogs, the influence of temperament in such problems as effective feed utilization, and the possibilities for similar investigations with other farm animals.

TURKEYS

Before the nineties, this country produced turkeys at the rate of 1 a year for every 5 persons. In subsequent years the blackhead disease, scourge of turkey growers, reduced this to 1 for every 15 persons. Recently research taught us how more nearly to control blackhead, and the number of turkeys has now risen to 1 a year for every 6.5 persons. But less scientific attention has been paid to breeding problems than to those of feeding, management, and disease control.

Our modern domesticated turkeys are descended from the North American or common wild turkey, of which there are five subspecies. Wild turkeys were apparently domesticated by the American Indians, and some of them were taken to Spain as early as 1498. Several European domesticated varieties were developed from this ancestry, and some of these were brought back to the colonies to become the foundation stock of our six present American breeds—the Bronze, the Narragansett, the White Holland, the Bourbon Red, the Black, and the Slate. The differences between these breeds are largely in plumage color.

Several major objectives stand out as desirable in turkey breeding, though little in the way of coordinated or intensive work has been done toward achieving them. (1) There is an increasing demand for a smaller bird to meet the needs of the average family. Hitherto, breeding has tended toward increased size. There is still a demand for large birds for hotels, etc., but they now actually sell at a discount because of the greater demand for smaller sizes. This situation can be corrected by breeding (2) There is need for improved body type to provide a larger proportion of meat to bone, especially on legs and breast. (3) Birds should be bred to reach market maturity at an earlier age. (4) Higher egg production is desirable, especially in making possible an earlier and longer laying season, which now covers a maximum of about 6 months. (5) Higher fertility and hatchability of eggs are desirable to reduce production cost. (6) Attention should be given to breeding for lower mortality, whether from disease or other causes.

In achieving such ends, use might be made of a breeding system based on production records, pedigrees and, progeny tests, such as that now used by progressive breeders of chickens. There is need for more trap nesting and pedigree recording to serve as a basis for isolating superior families and breeding from them. State and Federal agencies might well lead the way by developing strains notable for viability, quick maturity, and good market quality.

The small amount of genetic research with turkeys at State stations has been concerned with tracing the inheritance of plumage colors. The Department has experimented in making crosses between tur-

keys and chickens. All the hybrids died as embryos, though one lived almost to the hatching state. At its range experiment station in Montana, the Department carried on a 5-year inbreeding project which indicated the possibility of establishing inbred lines not inferior to outbred turkeys in fertility, hatchability, production, and weight of eggs. A similar outbreeding project was successful in improving fertility, hatchability, and production of eggs, and maintaining egg weight.

Ducks

There are places along the South Shore of Long Island, N. Y., where for many miles the air is filled with the quacking of ducks, and the creeks and small coves are white with the birds. This is the center of the commercial duck industry. The flocks are all Pekins, which are sold as "green ducks" at the age of 9 to 13 weeks, after a period of rapid fattening. Elsewhere in the country there are a few commercial duck farms, and ducks are raised as a side line on farms in every State. The Pekin is everywhere the outstanding breed, though the Rouen, Aylesbury, Cayuga, and Muscovy are also represented among the meat breeds; the Indian Runner among the egg breeds; and the White Call, Grey Call, Black East India, Mandarin, and wood duck among the ornamental breeds.

In the United States little has been done in the way of scientific duck breeding. Yet the best commercial flocks are remarkably uniform in the size and quality of the market birds, and remarkably efficient in fattening under good management; in 12 weeks they increase their weight 50 times. This uniformity may be in part due to the small number of Pekins in the original importations, from which nearly all the ducks of this breed are descended. As compared with chickens, the degree of inbreeding would be comparatively high, which would tend to make for homogeneity.

Duck breeders still rely entirely on their ability and experience in selection, and have not resorted to trap nesting, progeny testing, and the keeping of individual pedigree and production records. Mass matings are used exclusively, and the breeding birds are kept for only one laying season, on the ground that young birds lay earlier and are more prolific. These conditions preclude the keeping of individual records or the making of individual tests. Experimental inbreeding or cross-breeding is negligible or lacking, though the Aylesbury is sometimes crossed with the Pekin in England, and the mule duck, a cross of the Muscovy and the common domestic duck, is occasionally seen in this country.

In England trap nesting is practiced with the egg-laying breeds, and in the 16 years since individual records have been kept there has been great progress in improving egg production. The highest individual production runs over 360 eggs in a year, and there are many records of over 300 eggs. In egg-laying contests the average production per pound of body weight is much greater than is the case with chickens.

Ducks offer a virgin field for poultry-breeding research, especially in the inheritance of meat characters, since they are chiefly used for meat in this country. The same general principles should apply here as apply in the case of chickens. Research of this nature, however, is

not likely to be undertaken except in response to definite needs felt and expressed by those concerned in the industry.

Fur Animals

Breeding and genetic research is important in two ways in the conservation and improvement of fur resources. First there is the problem of maintaining the wild fur resources of the United States. There was a time when this country was the world's chief source of furs. Fortunes were made in the fur trade. Partly because of the lavish exploitation of fur animals, we no longer supply more than a third of our own needs. Meanwhile our demand for furs has increased, and little is done to conserve the fur animals we have left. An intelligent conservation policy requires, among other things, much more knowledge than we now have of the breeding habits and gestation periods of the animals in the wild. Studies of the marten made by the Bureau of Biological Survey, for example, show that this animal has a gestation period of 9½ months. This means that under any ordinary system of closed and open seasons, it would rapidly become extinct; in order to save the martens, it is necessary to prohibit trapping for several consecutive years. Similar accurate information on wild fur animals other than foxes is practically nonexistent.

The second need for research is in connection with the production of fur animals on farms. This is a rapidly growing industry in which an increasing number of farmers engage as a part-time enterprise. It is relatively very young, but it has now passed the early speculative stage and is settling down to a healthy basis. In 1923 the total value of silver fox pelts was less than $820,000; in 1936 it was over $8,000,000.

Fox farming has reached the stage where it needs the same kind of help from science that has long been given to other livestock industries. There is little in the way of a well-thought-out or scientifically tested procedure in present breeding practices. At the same time, fur color, which is the primary factor from the market standpoint, lends itself particularly well to inheritance studies and genetic analysis. A research project begun in 1928 by the Bureau of Biological Survey indicates what may be done in this direction. That study was an attempt to find out how the major types—the red fox; the standard silver fox, a mutation that occurred in Canada; the Alaska silver fox, a mutation that occurred in Alaska; and the cross fox, a hybrid between red and silver—behave in inheritance. Two pairs of genes, *A*, *a*, *B*, *b*, apparently accounted for these variations in color; and in breeding experiments, supplemented extensively from records of matings made by fox farmers, this genetic hypothesis worked out with remarkable accuracy, so that it was possible to tell, by referring to a genetic chart, just what results any given combination would give in a large population.

The Bureau is now engaged in a project to determine the inheritance of degrees of silvering in the pelts, since this is the fundamental basis of market classes. Both studies, however, have been limited by the small amount of funds available for such projects. There is need for more extensive research on this and other aspects of fur animal breeding by public agencies, both Federal and State.

Bees

The individual bee has such a painful and distracting way of making its personal importance felt that probably few of its victims have ever realized that in the United States bees are also the nucleus of a 35–50-million-dollar beekeeping industry, or that they give us much of our food supply by fertilizing blossoms. Both facts underscore the importance of breeding better bees.

The bee breeder, however, has a peculiar and in some respects an exceedingly difficult task. For example, he is confronted by at least five factors not faced by the breeder of other farm animals. (1) Bees mate in midair, and until recently it was impossible to make controlled matings, except in an uncertain way through the use of isolated mating yards. (2) The drone is produced by virgin birth and therefore receives its inheritance entirely from its mother. (2) The drone dies immediately after mating, and the queen mates only once in her lifetime; therefore their use in line breeding has been impossible. (4) The worker bee, which does the work of gathering and storing honey, is not fully developed sexually and therefore cannot be bred for a direct study of its inheritance, although it does at times produce males by virgin birth. (5) Identification of individuals and even races of bees often depends on very small points, which must be measured by special methods.

As a groundwork for breeding, it has been necessary (1) to study sex physiology and functioning, and (2) to develop physical measurements that can be used for identification.

The greatest hurdle was passed when methods were developed within recent years for artificially inseminating queens. This is now done in three ways—by taking spermatozoa from the male and introducing them into the female with a tiny syringe; by bringing about a compulsory mating between a queen and a drone, both held under constraint; or by removing the sex organs of the drone and inserting them in the queen. The first two methods were developed in the United States, the last in the Union of Soviet Socialist Republics. All three now involve the use of a microscope and delicate instruments. A limited approximation to line breeding may even be made by removing spermatozoa from a fertilized queen and introducing them into a daughter of the drone from which they originally came.

It remains to develop a technique for controlled mating under more natural conditions.

Progress has also been made in cataloging traits that will be useful in identifying individuals, tracing the effects of inheritance, and measuring colony behavior.

Meanwhile, without waiting for the uncertain appearance of useful mutations or for an exhaustive study of inheritance, the bee breeder is in a position to go ahead toward the goal of producing a bee better adapted to the needs of agriculture. He has several traits available in the germ plasm of the common black, Caucasian, Carniolan, Italian, and Cyprian races that it should be possible to combine—long tongue to reach deeper sources of nectar, gentleness, the tendency to make white comb cappings, reluctance to swarm, resistance to European

foulbrood and to common hive enemies, industriousness, and uniformity of body markings.

Some interesting but inconclusive work has been done on the ctyology of the honeybee. Genetic research has been scanty, but the inheritance of some characteristics has been studied, dominance and recessiveness has been determined for a few factors, and a few linkages have been worked out. It is known that Mendel worked with honeybees in his effort to determine the fundamental laws of inheritance, but unfortunately his notes have been lost.

Fundamentals of Heredity

Reproduction by means of sex involves the union of two cells, a male and a female, each of which carries a set of chromosomes containing large numbers of genes that determine hereditary characteristics. For example, when two parents with contrasting characteristics have been bred pure, the first generation resulting from their union has all the chromosomes and therefore all the genes of both parents. If a plant of this generation is selfed (the closest possible inbreeding), the characteristics of the original parent will begin to assort or segregate into groups among the offsprings of the second generation. The chromosome mechanism is such that all possible combinations come together if the number of second-generation offspring is large enough.

Thus beginning with the second generation, most of the progeny are not like either original parent but have different combinations or groupings of characteristics from both of them. In this wealth of new combinations of genes derived from two selected individuals, the breeder finds the particular combination he is looking for—or something that approximates it.

The segregation of characteristics occurs in definite ratios, first discovered by Mendel. They can be worked out mathematically from the fact that all possible combinations occur in a large number of progeny, but Mendel worked them out by observation and thereby found the clue to this fundamental law of inheritance.

A knowledge of the segregation ratios gives the breeder the clearest possible insight into the actual behavior of characteristics in inheritance, and in addition these ratios are of practical value in a number of ways. There are a great many different ratios because the effects of dominant and recessive genes, and various gene interactions, bring about many modifications of the basic numbers. The typical examples can be readily understood by patiently following, step by step, what actually happens in inheritance.

Other concepts constantly used by the breeder include linkage (the location of certain genes in the same chromosome), crossing over (the exchange of segments between two paired chromosomes), sex linkage (location of genes in the sex chromosomes), and mutations. All of these help to explain what actually occurs in nature and to define what the breeder can expect and what he cannot expect to accomplish.

Animal breeding does not lend itself to the same kind of neat and definite analysis for several reasons: (1) Selfing is impossible, and the closest inbreeding does not approach that in plants. (2) More progeny are required for many genetic analyses than can usually be

obtained with animals. (3) Most valuable characteristics in animals are quantitative (amount of milk produced, etc.), and such characteristics usually depend on relatively large numbers of genes interacting in complex ways. Nevertheless, there is an abundance of proof that animal inheritance works just like plant inheritance, and the basic concepts of genetics have been of enormous value in clarifying and improving animal-breeding methods. Even though the animal breeder will probably never be able to make the fine-spun analyses possible for the plant breeder, the newer knowledge of genetics is already reflected in animal-breeding practices, and it will undoubtedly make for more certain and more rapid progress, and fewer costly errors, on the part of those who will take the trouble to understand it.

Vegetative Reproduction

When plants are reproduced by means of cuttings, buds, tubers, runners, rattoons, or other vegetative parts, the breeding situation is different than when reproduction is by means of seeds.

A seed results from the union of two cells, male and female. Even if these come from the same flower or the same plant, many of the male and female cells will contain different chromosomal material unless the plant has been bred pure so that all its male and female reproductive cells have identical chromosomes. The differing chromosomes will be divided up among the progeny in such a way as to produce different types of individuals.

In reproduction by means of vegetative parts, there is no union of sex cells, and each new plant has precisely the same chromosomes as the plant from which it came. Exact copies of the original parent can be reproduced for any number of generations. Winesap apple trees have been reproduced by budding or grafting for many generations, and theoretically every Winesap tree today is exactly like its original ancestor of 200 years ago. Thus by the use of vegetative reproduction, all the trouble of "purifying" a strain is eliminated. Even the most mixed hybrid reproduces true to type. When this method is feasible, then, it is often a valuable short cut, especially where it is difficult- as in the case of many forest trees—to obtain true-breeding material from seed.

But occasionally the new individual is not exactly like the parent. Rarely, there are mutations in one or more genes in a vegetative cell, or some unusual behavior of the chromosomes, that make a part of the plant different from the rest. Usually this occurs only in one case out of several thousand. When the new form is valuable—as has been the case with some of the bud mutations of tree fruits—it too can be multiplied by means of vegetative reproduction.

On the other hand, this very ease of exact reproduction has limitations. The true genetic make-up of the breeding material is neglected; there is no need to know it, as there is in inbreeding and cross-breeding. Yet it is through the diversity of forms brought about by combining different chromosomal material that the modern breeder gets valuable additions to our economic plants. If he desires to make planned improvements, he must resort to seed production even with those plants that normally are reproduced by vegetative means. This has been amply proved, for example, in the case of potatoes and straw-

berries. By combining chromosomes, the breeder deliberately creates what he desires. When he uses vegetative mutations, he merely waits for nature to produce something that will be useful to him, trusting to trained observation to find it.

Do plants reproduced by vegetative means for many generations tend to run out or be weakened for the battle of survival? This has long been a popular belief. It may be said flatly that there is no real evidence that running out occurs. Where plants seem to run out it has been found in every case that the deterioration has been due to a virus disease or some other definite cause.

New Studies in Chromosomes

By studying the architecture of the molecule, chemists have been able to achieve marvelous results in synthesizing nature's products in the laboratory. How far geneticists may be able to go in this direction is not yet known, but new advances seem to be foreshadowed in the researches now being made on nature's methods of juggling chromosomes. Intensive study of the jimsonweed has been fruitful of knowledge in this field that may prove to have significant applications to breeding work with plants of economic value.

The present-day Mendelian analysis of inheritance, with its dominant and recessive traits, assumes that chromosomes go in pairs in the body cells. It is now known that they do not by any means always go in pairs. Rarely, there is only one of each kind instead of a pair. More frequently there are three or four of each kind, or even more. In some genera of plants, this arithmetical multiplication of chromosomes may run in a regular series, different species being characterized by different numbers of chromosomes in the set, though all the species in the genus have the same number of sets. This regular increase gives rise to what are called balanced chromosomal types, since the balance between the sets is maintained in spite of the additions.

But there are also unbalanced chromosomal types in which only a single set has an extra chromosome or chromosomes added to it. The balance within the cell is then disturbed; there is an excess of the material contained in the extra chromosome. Sometimes a complete extra chromosome or two is added to a set. Sometimes two identical half-chromosomes are added, joined together like a worm with a head at each end and the tails missing. Sometimes the addition is half of one chromosome and the opposite half of a chromosome from a different pair, joined together like a head and a tail from different worms. And so on.

Detecting this kind of jugglery within the cell might be interesting but academic if it were not for the fact that chromosomes carry the determiners of hereditary characters. Careful observation in jimsonweed shows that each of these changes results in specific alterations in the characteristics of the plant, both qualitative and quantitative. Large numbers of such changes have been classified and correlated with the addition or subtraction of whole chromosomes or different parts of chromosomes. The differences between races of jimsonweed in different parts of the world have been found to be due to rearrangement of chromosome material. In this way new kinds of chromosomes

have been produced, which have been used in building up new kinds of jimsonweeds. Types can be arranged in a regular series, and what effects will be produced by deleting or adding certain chromosome material can be predicted in advance.

From a practical standpoint, the significance of this lies in a possible increase in the controlled synthesis of plants of desired types. It suggests a somewhat different operation than that based on the usual analysis of unit factors alone. Cytological examination shows that many of our most valuable plants are characterized by unusual chromosome numbers of one kind or another. Can we repeat these deliberately, or bring about new and different additions and subtractions of chromosome material that will have significant effects? The experimental production of extrachromosomal types in jimsonweed is promising. Not the least interesting part of it is the fact that by suitable laboratory treatment of living cells such changes in chromosome material can be made to occur far more frequently than they do in nature.

Chronology of Genetics

The modern science of genetics is a fusion of several sciences and practices that for a long time developed separately—animal breeding, plant breeding, cytology, or the science of the microscopic cell, and certain branches of mathematics. If today men not only dare to dream of emulating and surpassing nature by creating new, improved forms of life, but actually do it on an ever-increasing scale, it is because they have a rich store of facts and theories on which to base their work—facts and theories contributed by patient researchers in many countries over many generations.

Both animal and plant breeding of a practical nature, of course, are very old, but all of the early work was hit-or-miss and uncertain, since it was not based on adequate knowledge. The first great milestone in modern genetics was the announcement by Camerarius of Germany in 1694 that plants reproduce by the union of male and female cells. This suggested deliberately uniting two different kinds of plants and was followed by the hybridization work of Fairchild in England about 1717, and of many others after him. It was not long (1727) before hybridization was put to commercial use by the Vilmorins in France, and by 1840 they were actually using a kind of progeny test. In 1859 Darwin put biological science on an experimental basis with his Origin of Species, and in 1866 Mendel in Austria worked out the mathematical laws of dominance, recessiveness, and segregation, previously observed but not interpreted by other workers. Mendel's paper remained unnoticed for many years, but meanwhile others were hot on the trail of the same conclusions. When his work was rediscovered in 1900, it gave a tremendous impetus to research and practical breeding alike. Shortly after this (1902–03), the observed phenomena of heredity were definitely and finally linked with activities within the cell.

The development of knowledge of the cell goes back at least to the time of Leeuwenhoek in the Netherlands, who first discovered the world of the microscope (around 1677). In 1838–39, Schleiden and Schwann in Germany generalized that all bodies are made up of cells;

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10 years later Hoffmeister in Germany actually saw chromosomes. In 1864, Nägeli in Switzerland was attributing the control of heredity to solid particles in the cell—an idea finally clinched by Weismann in 1892, after Haeckel, Strassburger, Flemming, Von Beneden, and others had developed more knowledge of the cell nucleus. From this time on the study of chromosome phenomena proceeded rapidly through the work of many cytologists, up to our own day when genes are accepted as the basis of inheritance and more and more of the facts of heredity are being checked against observed happenings in the cell nucleus. These developments have contributed also to an understanding of animal breeding, which on the practical side goes back through the work of Bakewell, the Collings, and others of a century ago, to Mago the Carthaginian, who in pre-Christian times developed the first known score card for livestock judging. Without mathematics, much of this knowledge would be unusable, and the work of many mathematicians has contributed to the exact interpretation of phenomena and to the practical application of theory.

Outstanding among recent developments are the identification of hundreds of genes in various organisms; the "mapping" of genes on chromosomes by genetic studies, and cytological proof of the actuality of these concepts; the use of the pomace fly for extremely fruitful genetic investigations; an understanding of many complex gene interactions that modify the original Mendelian laws; an increasing body of knowledge about chromosome behavior, which promises to open up new possibilities of practical control in breeding; and the beginnings of knowledge, through the use of X-rays and other forms of wave energy, of how basic changes in genes and chromosomes are brought about, so that controlled genetic change becomes a speculative possibility.

The most recent developments indicate that new researches in biological chemistry may in their turn throw light on some of the many unsolved secrets of the gene and its control of heredity.

VEGETABLE CROP BREEDING AND IMPROVEMENT—AN INTRODUCTION

VICTOR R. BOSWELL, Principal Horticulturist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry

IN CONTRAST with the comparatively small number of different species of important extensive farm crops—a half dozen cereals, two fiber crops, two sugar crops, and perhaps a dozen forage crops—literally scores of common vegetable-crop species are widely grown over this country. The scientific basis for orderly and efficient breeding of most vegetables is much less highly developed than in the cereal and sugar crops, for example, and therefore less can be said concerning the genetics of most individual vegetable-crop species. Even so, the large number of crops to be considered compels drastic limitation of subject matter and scope of the articles that follow.

FEW FOREIGN VARIETIES ADOPTED IN THE UNITED STATES

THE excellent and comprehensive treatments of wheat, corn, and certain other crops in the 1936 Yearbook of Agriculture include much data upon foreign varieties, breeding, and improvement; but for many of our vegetable crops such information either is not available or is of such limited interest in the United States that its compilation and publication are hardly practicable. In the main, foreign varieties of vegetables either do not appeal to our tastes or are not well adapted to the environment and the methods of handling in the United States. There are noteworthy exceptions, of course, for there is some international agreement in consumers' tastes and a few crops show wide ranges of adaptability. But the activities of foreign workers have thus far remained to a a large extent of academic interest to us, except insofar as they dealt with basic problems of genetics or plant culture. A few examples will explain our limited use of foreign productions.

England stands preeminent in the improvement of the garden pea. More of our pea varieties (or their parent varieties) originated there than in all other countries combined. The English climate is quite cool and moist, ideally adapted to the garden pea, which is sometimes called the English pea. Even though many of our varieties are readily traceable to English work, they constitute only a fraction of the number that have been produced and are still grown in that country. Most of the English varieties are not at all adapted to our more extreme and changeable climate. Most of our own varieties of peas are inferior in quality to the English varieties as these are grown in England.

Tomatoes are grown in England almost exclusively in greenhouses. None of our important commercial sorts will bear satisfactorily out

contribution to vegetable improvement. As has been pointed out for other kinds of crops, they have devised shorter and more effective methods of improvement that are gradually coming into general use by commercial agencies. The Federal and State workers have also accomplished incalculable benefits by the simple procedure of developing superior stocks of old varieties by selection, freeing stocks of mixture and disease, and releasing the resulting material into trade channels. Some of the best and latest productions will not be generally offered for sale for another year or so.

NEW INFLUENCES IN VEGETABLE IMPROVEMENT

Although the avoidance of contamination with disease is perhaps the foremost consideration in seed certification by several States, certification also relates to trueness to varietal type and freedom from rogues and mixtures. This certification does not involve original breeding or improvement but does compel the application of up-to-date methods of maintaining advances that have been made by breeders. Certification, therefore, deserves mention as a public service closely allied with improvement. From a practical standpoint it has resulted in very substantially raising the standards of performances of tens of thousands of acres of vegetable crops.

Under authority of the Bankhead-Jones Act, passed in 1935, the Division of Fruit and Vegetable Crops and Diseases is developing near Charleston, S. C., a well-equipped vegetable breeding laboratory for the study of fundamental breeding problems that are basic to the production of new and improved varieties for the South and Southeast. Solutions to these problems of national and world interest will of course be forthcoming. Rapid progress is being made in providing facilities for research, and a small but able and active staff has been at work since the spring of 1936. The establishment of this station, the only one in this country devoted exclusively to vegetable breeding, is a particularly significant step, but is only one of the signs of the times. The study and application of genetics are certain to solve an increasing number of our problems and contribute greatly to the general welfare.

Another station in the United States that may well be expected to make unusual contributions is the Great Plains Horticultural Field Station, of the Division of Fruit and Vegetable Crops and Diseases, at Cheyenne, Wyo. A most extensive collection of thousands of domestic and foreign varieties, strains, and stocks of vegetables has been acquired by that station in the quest for characteristics of earliness, drought resistance, and cold resistance. Vast stretches of our western United States have such a short growing season by reason of high latitude or altitude, and such extremes of temperature, with low humidity, drying winds, and short water supply, that only a very meager list of vegetable varieties can be grown. There is pressing need for either introducing or breeding varieties of nearly all crops for home and local market use by people living in those areas. The staff of the station at Cheyenne includes men highly trained in horticulture, genetics, cytology, and physiology. The joint efforts of all are directed to the examination of promising material and the execution of a breeding program designed to meet the requirements of the region.

The Division of Plant Exploration and Introduction of the Bureau of Plant Industry plays an important part in the breeding programs, not only of Federal agencies but of all the State experiment stations that call upon that Division for help. Their information upon the geography of plants, their constant close contacts with investigators and dealers all over the world, their exploring expeditions into obscure places, combine to make available to plant breeders in this country a wealth of the world's plant materials that is remarkable. And naturally the Division assists foreign investigators by supplying in exchange considerable quantities of material from American collections. The world's supply of plant materials is becoming diffused into all countries for anyone to use who will.

PRESENTATION OF SUBJECT MATTER

A FEW words are in order with reference to the organization of subject matter in the articles on vegetable breeding. It is obviously impracticable to treat each crop extensively, therefore crops have been grouped for treatment. Groups are based on botanical and structural similarities in most cases, but a few on the basis of similarity of use or purpose for which they are grown. This grouping has been adopted purely as a matter of convenience in compiling the information or for presenting together crops of related interest regardless of botanical relations. It is not to be considered as a scientific classification. In most cases the authors of the respective articles are now conducting breeding or genetic investigations or have had special breeding experience with the crops under discussion.

It will be noted that the appendix to this group of articles (p. 340) contains data on a number of unclassified crops not discussed in detail in the articles, such as peanuts, sweetpotatoes, and others. Definite information on the breeding, improvement, and genetics of these crops is indeed meager despite the great economic importance of some of them. There is practically no exact knowledge about inheritance in the sweetpotato, and even the origin of surprisingly few sorts is known. The peanut until quite recently has been almost ignored by scientific breeders and students of genetics, but it is due for increasing attention.

IMPROVEMENT AND GENETICS OF TOMATOES, PEPPERS, AND EGGPLANT

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TOMATO

INSOFAR as we are able to tell from written record, the tomato is a very new crop (*18*).[1] The oldest records of it date back less than 400 years, a brief time when compared with the oldest available records of many other crops. The tomato is of tropical American origin, and early reports indicate that it was planted in maize fields and eaten by the ancient Mexicans, who called it tomati. Apparently it attained no very important place in the lives of those people, perhaps on account of the highly perishable nature of the edible fruit and the absence of known means for its preservation. Although it is believed to be native to the same regions as certain early forms of maize, there are no known prehistoric remains, no prehistoric sculpture or ceramics to record its early culture as in the case of maize, kidney beans, lima beans, and squash in North America, or wheat and numerous other plants in the East. We thus are able to form no definite idea of its antiquity and early importance. The absence of record or remains of plant parts might imply relative unimportance and little use. On the other hand, the earliest references in the literature describe essentially the same forms that are grown today. No new markedly different fruit types are known to have appeared since, and the large forms have never been found truly wild. It is therefore believed that the tomato was already improved far beyond the wild state when North America was discovered. Even so, our smooth, large, symmetrical-fruited varieties of today are in marked contrast to the rough, variable types known in this country a century ago.

We have all heard how the able, up-and-coming young man is rarely appreciated in his native environment but must go abroad to make good, and then returns to receive the approval of his countrymen. Some of our native American crops, including the tomato, have gone through a similar experience. The potato, native to the New World, is called "Irish potato" because colonial America repatriated it to the New World from Ireland, where it had become a very important crop while it was being ignored close to its native land. The tomato was introduced into Europe early in the sixteenth century and became widely distributed. In the seventeenth century it was grown in England for ornament only, although it was known to be eaten elsewhere. By the end of the eighteenth century it was grown

[1] Italic numbers in parentheses refer to Literature Cited, p. 204.

on a field scale in Italy and used extensively as food, but it was a half century more before people in the United States generally dared to eat it.

Early Varietal Adaptation

Although each of several countries in which tomatoes are grown to any large extent usually has a number of varieties that show a considerable range in varietal characteristics among themselves, the group of varieties grown in each region is rather distinct from those grown in certain other parts of the world. Not every country has its own distinct general type, but there are marked differences between geographic areas. It is probable that definite selection and breeding work with the tomato for adapting it to warm-temperate and cool-temperate regions has been in progress but a short time, not over two centuries and perhaps only half that. Nevertheless, in a certainly brief span this tropical or subtropical plant has been adapted to a wide range of environments far different from its native home. The efforts at selection by early growers of the crop together with natural factors produced a very interesting and effective assortment of general types, each of which apparently points toward the maximum adaptability in each region.

The best Italian varieties in general are of long season and are large, vigorous growers, with a profusion of thick-walled fruits of unusually brilliant color and high content of solids. A wide range in fruit size exists among these varieties, some of the most valuable being small, as judged by United States preferences. The important point is that those varieties do better in Italy than elsewhere and are better for Italian purposes than others that have been tried in Italy.

There is a considerable outdoor culture of tomatoes in Germany and some adjacent north-European areas. The varieties grown there are early, relatively small-vined, and medium- to small-fruited.

THE *early tomato breeders did excellent work in producing plants with good yields of large handsome fruits, adapted to local or regional conditions; but the situation has changed, and new problems and requirements have arisen so fast that it is not now possible to keep ahead of them by the old method of selecting chance variants in the field. Systematic effort is necessary to find and bring together characteristics that will make entirely new varieties resistant to specific diseases and to heat and cold, and adaptable to long-distance shipment, to new areas of culture, to new processes or means of utilization. This is the kind of work being done by State and Federal agencies. The disease problem especially is so important today that practically no research agency would introduce any new variety unless it were resistant to at least one very troublesome disease.*

Italian and most United States varieties are not adapted to the climate of Germany, and the German varieties when grown in the United States are distinctly inferior to our own. Except for color differences, the north-European sorts are largely of the one general type described.

As mentioned in the introductory article on vegetables, the English have developed a characteristic type of greenhouse tomato, some varieties of which are practically parthenocarpic, requiring no pollination, by hand or otherwise, as American varieties do, in order to set fruit. These varieties are very prolific, setting very large numbers of fruits that are too small to suit American growers and consumers—but they are well adapted to the region and to the purpose for which they are grown. They were the first improved varieties in the modern sense.

In a large country like the United States, with a climatic range from subtropical to cool temperate and from humid to arid, different variety groups have been developed to suit different parts of the country. Until about 10 years ago most of this adaptation had been effected by private growers and seedsmen, who selected chance variants or the progeny of natural crosses that were particularly promising in a given region. A few of the old important varieties were the results of artificial hybridizing. Extensive commercial tomato production in this country is not much over 50 years old. Sixty years ago the only large sorts were rough, ugly, heavily ribbed, variable "varieties" of indifferent quality, although some good small ones of the greenhouse type had been brought in from England.

The old varieties were certainly quite heterozygous or mixed in their hereditary composition, for the tomato frequently crosses naturally in the field. Bailey (*3*) and others have referred to tomato varieties running out. These cases were doubtless due to the effects of more or less accidental selection within very mixed populations. These few rough and ready mixtures, our early so-called varieties, were the confused mass of raw material from which so many of our really good varieties have been selected, directly or indirectly, by keen-eyed growers. Tomatoes are now grown commercially in every State in this country.

Improvement in the United States, 1850–1910 [2]

Prior to 1860 no tomato varieties had been developed in the United States. The few varieties known had been brought in chiefly from England and a few from France. It appears that most of the large-fruited varieties, if not all of them, had been obtained by selection from the old Large Red or ribbed type that had been known since about 1550. The smaller fruited, more prolific forcing or greenhouse types and similar sorts presumably were first selected from the round tomato (smooth), which was originally described by Tournefort about 1700. Since there has been only a minor interest in the small-fruited forms in this country, a chronology of tomato improvement will be confined largely to the story of the old Large Red and its descen-

[2] In the preparation of this historical review the writer has freely used unpublished notes and records in the files of the Division of Fruit and Vegetable Crops and Diseases made by the late W. W. Tracy, Sr., and by D. N. Shoemaker and other former staff members.

dants. The old Round, however, has apparently contributed some genes of value. The cherry-, pear-, and plum-shaped tomatoes have been known as long as the Large Red but have undergone no appreciable change.

Probably the first true dwarf or "tree" variety, named Tree, was introduced by Vilmorin-Andrieux & Cie., of Paris, in 1860, and was promptly brought into this country. It was found as a chance variant in a tall variety by a private gardener of an estate at Chateau de Laye in France. Two other imported varieties of interest in the United States, introduced about that time, were Fiji Island (1862) and Cook Favorite (1864). Several forcing types of European origin were being grown, but their origin is obscure.

Probably the first United States contribution to tomato improvement was the introduction of the Tilden variety by Henry Tilden, of Davenport, Iowa, in 1865. It originated as a chance seedling in a field of a variety the name of which is not recorded (*3*).

The next notable advance occurred in 1870 with the introduction of Trophy, a result of hybridization and selection by a Dr. Hand, of Baltimore County, Md. It is said to have been from a cross of Large Red × Early Red Smooth. The variety was introduced by G. E. Waring, of Newport, R. I., who received it as a supposedly fairly well-fixed stock from T. J. Hand, the son of the originator. It has been stated that Trophy was involved in the parentage of most of the varieties introduced in the following quarter century, and undoubtedly it has contributed, at least indirectly, to a great number of later varieties. The old original Trophy was evidently not very well fixed, however, for before 1900 it had practically ceased to exist (*3*). Through both purposeful and accidental hybridization, and through artificial selection and natural selection within a rather heterozygous variety, superior variants were saved and inferior ones discarded. There is evidence, too, that the perpetuation and increase of undesirable variants appearing in the variety (running out) as a result of segregation, natural crossing, mechanical mixture, or combinations of these, hastened the demise of the variety.

Figure 1.—A. W. Livingston (1822–98), pioneer tomato breeder of Columbus, Ohio, who developed many tomato varieties still in current use.

The work of A. W. Livingston (fig. 1), of Columbus, Ohio, and his associates and successors in the Livingston Seed Co. has resulted in the introduction of more new varieties than that of any other private group. Most of the varieties introduced by the Livingstons were of their own

finding or origination, but some were obtained from other growers. Paragon, from a chance seedling, was their first introduction (1870).

The famous old variety Acme was developed by A. W. Livingston from a single superior plant found in a field of mixed stock and introduced in 1875. Like the Trophy, this variety was the source or served as one parent of many subsequently introduced varieties. In 1880 Perfection, a chance variant in Acme, was introduced. Livingston next brought out Golden Queen in 1882, Favorite in 1883, Beauty in 1886, Potato Leaf in 1887, Stone (4) in 1889, and Royal Red in 1892. This last was developed from seven similar plants found in a field of Dwarf Champion by M. M. Miesse. The others just named were chance seedlings occurring in varieties the names of which are not known. These were followed by Aristocrat and Buckeye State in 1893, Honor Bright in 1897, and Magnus in 1900, as chance seedlings in varieties not recorded. In 1903 Dwarf Stone was introduced; it was a chance seedling found in Stone. Globe (4) is from a cross between Stone and Ponderosa made about 1899 by Robert Livingston and was introduced in 1905. Hummer, another introduction, was selected out of Paragon.

Of this impressive list introduced by the Livingstons, Stone and Globe are among the most important varieties grown today. Acme, Beauty, Buckeye State, Dwarf Stone, Golden Queen, and Perfection are still listed by some seed producers although they are not extensively grown.

In 1882 D. M. Ferry & Co. obtained a selection made by a farmer grower from an unknown variety, and they introduced it in 1885 as Optimus.

Some introductions of W. Atlee Burpee & Co. were Matchless, introduced in 1889; Fordhook Fancy, a production by E. C. Green, of the Ohio Agricultural Experiment Station, in 1898; Combination (Lorillard × Acme × Comet) in 1896; and Quarter Century in 1899—a cross between Lorillard and Dwarf Champion. These last two were developed by Walter Van Fleet, then of the Rural New Yorker.

In 1887, at the Michigan Agricultural College, L. H. Bailey selected a single outstanding plant from a plot of a German variety, Eiformig Dauer. This was released as the Ignotum variety and proved to be of major importance for many years.

Several varieties that had attained importance prior to 1910 are either of obscure parentage or their parentage has been reported and the introducer's name is not definitely known. Lorillard, named for its producer, was introduced in 1888 and was said to be from a cross between Acme and Perfection. The following are of unknown parentage: Chalk Early Jewel, by Moore & Simon in 1900; Ponderosa, by Peter Henderson in 1891; Early Detroit (4), from seed obtained from a Mr. Rosendahl, of Fort Leavenworth, Kans., introduced in 1909 by D. M. Ferry & Co.

The Stone variety has been the supposed parent stock of several varieties of considerable importance, among them Dwarf Stone, mentioned above; Earliana (4), found by George Sparks, of Salem, N. J., and introduced in 1900 by Johnson & Stokes; Greater Baltimore (4), found by John Baer, of Baltimore, Md., and introduced by J. Bolgiano & Sons in 1905.

Johnson & Stokes introduced Bonny Best (*4*) in 1908. It came from a single plant selection in a field of Chalk Early Jewel by G. W. Middleton, of Jeffersonville, Pa.

With all due credit to the important contributions of other growers seedsmen, and investigators, it is not out of place to call attention again to the great contribution of the Livingston Seed Co. to tomato improvement. Of about 40 varieties that had attained a distinct status prior to 1910, a third were productions of or introductions by the Livingston company. If we add those varieties derived directly from Livingston productions and introductions, it appears that half of the major varieties were due to the abilities of the Livingstons to evaluate and perpetuate superior material in the tomato.

Private Introductions, 1910–36

Due credit must be given the early workers mentioned in the preceding pages. Their object was to get good yields of large handsome fruits borne by plants adapted to local or regional conditions, and they succeeded admirably—so well, in fact, that about half of the 40 important varieties known in 1903 are still listed by at least a few of the larger producers and dealers. A few varieties, notably Chalk Early Jewel, Earliana, Ponderosa, Stone, and the dwarf sorts are universally listed. This older type of effort still continues, and from time to time some quite worth-while strains result from it. In comparison with the period 1875 to 1900, however, the old method of selection and crossing among present commercial sorts has in recent years resulted in a smaller number of marked improvements. Many of those obtained have been of value, particularly with respect to regional adaptation and suitability for long-distance shipping or for manufacture.

The Cooper Special, a variety with a distinctive, determinate, or "self-topping" habit of vine growth, was introduced by C. D. Cooper, a farmer near Fort Lauderdale, Fla. It was found as a chance seedling by Bert Croft in Florida in 1914.

Grand Rapids Forcing, long a popular greenhouse variety, was produced by John Nellist, a grower near Grand Rapids, Mich., by crossing Bonny Best and Comet, an English variety.

In 1915 John Baer, of Baltimore County, Md., turned over a selection from Bonny Best, which was named John Baer, to J. Bolgiano & Sons for introduction. Although similar to Bonny Best in many respects, this strain or variety seems particularly adapted to the northeastern group of tomato-growing States and is often preferred to other stocks offered under the name of Bonny Best.

In 1920 the Everett B. Clark Seed Co. introduced an early shipping variety, named Clark Early, for culture mainly in the South. It was obtained by selection. D. M. Ferry & Co. in 1921 introduced Gulf State Market, a variety very similar to Globe but a trifle earlier in the South and less susceptible to cracking. It was found as a single plant in a field of Early Detroit by Walter Richards, of Crystal Springs, Miss., in 1917.

The J. T. D. is an interesting example of a local type developed for adaptation to a specific set of conditions and needs. It was developed

by the Campbell Soup Co. for growing in New Jersey, mainly for its own factory use. It has not become widely grown elsewhere.

In addition to these rather distinct sorts, several commercial firms and seed growers have given special attention to the isolation of superior stocks and strains of a number of the leading commercial varieties. Some of these stocks have been introduced under new names but frequently with only slight variation in the accepted name. A new name or a modified name does not, of course, insure improvement or even a difference. It may fairly be stated, however, that a number of these carefully handled "special" commercial strains of well-established varieties have proved to be superior to stocks generally available under the common name.

Improvement by Public Agencies

A discussion of the research that makes possible more rapid and orderly improvement of the tomato will be found in the section on Studies of Inheritance and Cytology at the end of this article. At this point will be presented a historical review of the new varieties introduced by State agricultural experiment stations and the United States Department of Agriculture.

In the last 25 years new problems and requirements have arisen so fast that tomato breeders cannot find naturally occurring chance variants with the desired characteristics fast enough to keep ahead of requirements. Special efforts are necessary to find and bring together these newly required features to produce new combinations, entirely new and different varieties. Of course the old objectives of large, smooth, high-quality fruit and high yields are still sought, but they must be in combination with such factors as tolerance or resistance to specific diseases, to heat, to cold, and adaptability to long-distance shipment, to new areas of culture, and to new processes or means of utilization. These characteristics are difficult to find and combine quickly with other desired properties.

Introductions prior to 1910 by public agencies were few and far between. Reference has already been made to Ignotum, selected by Bailey at the Michigan Agricultural College, and Fordhook Fancy, produced by Green at the Ohio station.

The major part of the tomato breeding by State and Federal agencies has been done in efforts to develop varieties resistant to disease. Thus far most attention has been devoted to resistance to fusarium wilt (fig. 2), but resistance to other diseases has also been sought, namely, nailhead rust, leaf spot, leaf mold, mosaic, and curly top. The disease problem in general has become so important that today there is little inclination on the part of research agencies to introduce any new tomato variety unless it is resistant to at least one very troublesome disease.

Selection for resistance to fusarium wilt was first started in 1910 by Essary (*15*), of the Tennessee Agricultural Experiment Station, and by Edgerton (*13*), of the Louisiana station. Two years later Essary distributed a resistant strain of the general type of Beauty but with a scarlet fruit like the color of Stone. This new sort, developed by mass selection from a diseased field near Gibson, Tenn., became known as

Tennessee Red. Later Essary distributed a wilt-resistant variety with scarlet-red fruit, named Tennessee Pink, also developed by mass selection in seriously diseased fields. Edgerton, in Louisiana, announced his first wilt-resistant sort in 1912. It was called Louisiana Wilt Resistant and was developed from a single resistant plant selected in a badly infected field of Acme.

Although Louisiana Wilt Resistant proved highly resistant to the disease, it was late and a poor yielder. Edgerton crossed it in 1912 with the Langdon strain of Earliana to get earliness and fruitfulness. From the progeny of this hybrid a scarlet and a scarlet-red strain—

Figure 2.—A comparison of wilt-susceptible (*A*) and wilt-resistant (*B*) varieties of tomatoes on heavily infected land.

commonly called "red" and "pink", respectively—were isolated, named Louisiana Red and Louisiana Pink, and distributed about 1918.

Norton (*40*), of the Maryland station, began selection for wilt resistance in 1912, selecting from a large number of varieties grown near Preston, Md., on a field naturally heavily infected. A number of unnamed resistant selections were distributed in 1915 to tomato growers and investigators. One of these, a wilt-resistant strain of Greater Baltimore, was further selected and grown for seed for several years by O. W. Twilley, of Hurlock, Md. In 1912 Norton selected a wilt-resistant sort from a field of badly damaged mixed varieties near Vienna, Md. This was included among strains given in 1915 to F. J. Pritchard (fig. 3), of the Department of Agriculture, who started his disease-resistant improvement work in that year. Two years of fur-

ther selection in this strain by Pritchard resulted in the Norton variety, distributed in 1917 by the Department and named for the man who made the original resistant plant selection. Two other resistant strains that Norton gave to Pritchard in 1915 were selected by the former from fields of Greater Baltimore. Pritchard selected them further under conditions of heavily artificially infected soil and distributed them in 1918 under the names of Columbia and Arlington. These three varieties, Norton, Columbia, and Arlington (*42*), developed by the informal joint efforts of the Maryland Agricultural Experiment Station and Department workers, were widely disseminated and were the leading resistant varieties, particularly in the East, for some years.

Pritchard distributed a third improvement in 1918 under the name of Marvel. He obtained it by selection from a French variety, Merveille des Marchés (Marvel of the Market), which shows a rather high and fairly uniform resistance (*42*).

Figure 3.—F. J. Pritchard, of the United States Department of Agriculture, who did notable work in breeding improved disease-resistant varieties of tomatoes.

Since 1917 the wilt-resistant varieties produced by the Department have greatly predominated over those originated by others. For reasons not entirely clear, those produced by various State experiment stations have remained more or less localized, and the total acreages of them are not very great. It may be that in the course of production and testing the limited opportunities of determining wide adaptability resulted in selections that were especially adapted to a rather narrow range of conditions; or it may be that the larger resources of the Department made possible not only more extensive tests but larger supplies of seed for original distribution and more effective dissemination of information about the new sorts. It seems probable that some of the State work has resulted in varieties quite the equal of the Department sorts now commonly grown, or even superior to them in some respects, but still the latter dominate the field.

It should be recognized here that some of the first stocks of certain Department varieties distributed were the result of massing a number of selections that were apparently similar under the conditions of selecting. Under other growth conditions, undesirable variations in fruit and plant form appeared. Numerous State and private agencies have contributed to the success of these varieties by careful roguing or selection within the early stocks, keeping them in closer conformity to the ideals for the respective sorts.

In 1922 Pritchard introduced Norduke, a cross (Norton × Duke of York) between two resistant sorts. Marvana (Marvel × Earliana) and Marvelosa (Marvel × Ponderosa) followed in 1924. All these earlier introductions by the Department are still listed by commercial firms (most firms list only one or a few of them), but they are unimportant and are not generally grown except in certain localities. Subsequent superior productions have largely displaced them.

The Marglobe (*4*), introduced by Pritchard and Porte in 1925, is without doubt the most important variety of tomato in the United States and in the world today. Its range of adaptability to both environmental and utilitarian requirements and its dominant position have been surprising. Marglobe is the result of a cross between Globe and Marvel made in a greenhouse of the Department in Washington in 1918. Globe has considerable resistance to wilt but is very susceptible to nailhead rust. Marvel is highly resistant to both. Marglobe proved highly resistant to wilt under most conditions and to nailhead under all conditions of which there is record. It was introduced just in time to save the Florida tomato-shipping industry from virtual extinction through the ravages of nailhead and wilt. It was developed primarily as a shipping tomato, but it has turned out to be the principal canning variety in the Middle Atlantic and South Atlantic States, as well as the leading shipping variety of the whole Atlantic region. It was the dominant variety in Mexico during the heyday of the tomato-shipping industry in that country; it is one of the best varieties recommended in Australia, and it is currently listed by commercial vegetable seedsmen in many foreign countries. The Marglobe has been to the present generation what Trophy and Acme were two generations ago. But ultimately, perhaps before long, it will be superseded by still better sorts, for, like all varieties, it has its limitations. It cracks rather badly, particularly in the Middle West, and it is not appreciably resistant to a number of diseases that are becoming increasingly important.

Three more recent productions by Pritchard and Porte should be mentioned before returning to some of the earlier work of the State stations. Marglobe was a parent in two of these—Break o' Day (Marglobe × Marvana), introduced in 1931, and Pritchard [3] (Cooper Special × Marglobe), introduced in 1932. Break o' Day was received much more enthusiastically than Pritchard, as a result of preliminary trials; but it has subsequently slipped into a relatively unimportant place, largely because it fails to meet rigid color requirements under most conditions. Pritchard, however, has become very popular on account of its superior scarlet color, despite the fact that it tends to bear most of its crop in a short time. It was expected to be of no value to canners because of this habit, but it is being used more each year. The third variety, Glovel [4] (Globe × Marvel), is a "sister" to Marglobe but is scarlet-red ("pink") instead of scarlet ("red"). It is otherwise rather similar to Marglobe and is especially interesting because it cracks much less than Marglobe. Although reports on it

[3] Introduced under the name of Scarlet Topper. Renamed Pritchard in 1932 after Pritchard's death in January 1931.

[4] Produced in cooperation with the Florida Agricultural Experiment Station.

are generally good, it is too early to determine its value, since it was introduced in the spring of 1935 and first grown commercially in 1936. These last three varieties are all resistant to both fusarium wilt and nailhead.

The most important variety in the middle-western canning area of Illinois and Indiana is the Indiana Baltimore, developed by the Indiana Agricultural Experiment Station by selection from Greater Baltimore and distributed in 1919. It represents a distinct improvement over its parent variety, although the casual observer would consider it similar.

Yeager (*54*), of North Dakota, has done some of the most interesting tomato breeding in this country, but his work is not generally known and appreciated outside the northern Great Plains area. Yeager has bent his efforts to the development of a list of varieties adapted to a short, rather dry season in a region of wide extremes of temperature and frequent desiccating winds. These conditions are decidedly unfavorable for tomatoes in general. It is only in the last 12 years that farmers and gardeners of the northern Great Plains have had varieties that could be grown there with any satisfaction, but now they have several. Even though these varieties from the North Dakota station are adapted to the area in question and are far better there than anything heretofore available, they are of little interest elsewhere. The very characters that enable them to succeed in North Dakota appear valueless, for example, in Virginia. That, however, is no discredit to the varieties or the introducer. They serve the purpose for which they were bred, and that is enough.

The seven varieties introduced by Yeager up to this time are all early and bear their moderate crops on comparatively small plants in a short time. This is necessary in order to meet the requirements of the region. All were developed by hybridization, one of them involving an interspecies cross. Red River (Earliana × Sunrise), introduced in 1925, and Bison (Red River × Cooper Special), introduced in 1929, are the best known and most important thus far. The latter has shown an appreciable resistance to heat. Two yellow varieties, Fargo Yellow Pear (Bison × Yellow Pear) and Golden Bison (Bison × Golden Queen), introduced in 1932, meet the requirements of those gardeners who desire yellow-fruited sorts. Farthest North is of particular interest because of its parentage (Bison × Red Currant) and its extreme earliness. It was introduced in 1934, so it may be rather too new to tell how important it is going to be. The other two of Yeager's introductions are Early Jumbo (June Pink × Globe), distributed in 1929, and Pink Heart (Bison × Ohio Red), distributed in 1932.

The Santa Clara (*4*) tomato, which is now the principal variety grown for canning in California, is the result of work by several agencies and men. It traces back to a single plant selection made in 1923 by a representative of the Canners League, in a field of a variety called Trophy or Canner. This was not the old original Trophy previously mentioned, nor even the variety generally cataloged under that name by seedsmen. It was a large, irregular, rough-fruited sort that was wasteful and difficult to prepare for canning on account of corrugations

and catfaces, and was grown only for canning in that section. The Canners League, the Ferry-Morse Seed Co., the California Packing Corporation, and the California Agricultural Experiment Station all contributed to the further selection and final development of this huge, moderately smooth-fruited variety that entered into commercial production about 1926. It has a very large heavy-yielding plant that produces the largest fruits of any of the extensively grown commercial sorts, but anyone who tries to grow it east of the Rocky Mountains will be disappointed in it. It is excellent in parts of California but almost a failure in other parts of the country.

In 1928 the California station released a selection from Santa Clara developed through careful inbreeding and called California 55. It was produced for its smoother fruits, high yield, and more intense red color.

The Illinois, Massachusetts, and Michigan stations have placed emphasis on greenhouse sorts because of the magnitude of the forcing industry in their States. In 1930 Illinois introduced Lloyd Forcing and Blair Forcing, both derived from Louisiana Pink × Grand Rapids. Both varieties are wilt resistant. In 1931 Massachusetts introduced Waltham Forcing, a selection from an unknown sort for adaptation to adverse northern greenhouse conditions.

The New Jersey station distributed the Rutgers variety in 1934. It is a cross of Marglobe × J. T. D. and has been reported especially valuable on the light sandy soils of New Jersey. The Illinois station has just released sorts that will set fruit and not grow out of bounds on the high-nitrogen praire soils of Illinois. The Washington (State) station introduced in 1930 Seedling 36 and Seedling 50, results of crossing Bonny Best × Best of All to obtain higher productivity under Washington conditions. They were intended to be adapted to a specific environment, hence it is not surprising that they have remained of rather local interest.

Within the last year or two many stations have released several additional strains and varieties that may or may not make important places for themselves. Small plot tests, even though numerous and fairly widespread, often fail—in fact usually fail—to reveal the true commercial possibilities of a new line and to indicate the reactions of the tomato-growing industry and the consuming public. Only time and general commercial trial can determine these things. The newer introductions, as reported by their originators, are listed in table 4 of the appendix to the vegetable articles, along with those discussed in this brief survey.

Gratifying progress has been made in the selection of verticillium and fusarium wilt resistant strains of tomato in California by Michael Shapovalov, of the Department, and B. A. Rudolph, of the California station, working cooperatively.

PEPPERS

History

The hot and the sweet peppers grown in the United States belong to a quite different group of plants from the black or white pepper of commerce. The peppers that we grow in this country are *Capsicum*

annuum L., a New World species native to the Tropics. There are no ancient eastern names for the species, and the first record of it (1493) indicates that Columbus took the first specimens to Europe on returning from his first voyage to the West Indies. Peppers or chilis are known to have been one of the principal foods of the native inhabitants of tropical America. The pepper had already reached a fairly modern state of improvement at the time of its discovery by Europeans, as evidenced by the wide diversity of the several distinct sorts described in the early records. All the types current today were known to be used by the natives of Central America in the seventeenth century (*18*). It would thus seem that the prehistory of the pepper might closely parallel that of the tomato.

There seems to have been no such aversion in Europe and colonial America to the use of peppers as there was to tomatoes. Peppers were apparently adopted immediately, and their use quickly became almost worldwide. Certain types became established so promptly in India, for example, that some of the early botanists believed them native to the East. However, the name "chili", which is still used in India, strongly indicates importation from South America.

Although they were quickly adopted and have been generally used beyond their native land for over 400 years, the properties of most varieties of peppers do not make them a product to be eaten in large quantities as a staple vegetable by most users. Generally peppers, even the sweet or nonpungent varieties, form a small proportion of salads or mixed vegetable dishes. Some nationalities, however, use them more or less "straight", the Mexicans in particular consuming almost incredible quantities of them. And those who are familiar with Mexican cookery know how generously the fiery varieties are used.

Improvement in the United States

Since the pepper is not a major crop, it has received far less attention than its relation the tomato. Even though a few enthusiasts have effected some excellent improvements, the importance of the crop itself has not been great enough to attract much attention to more than a few of the advances made. As a result, the records concerning early improvement are very sketchy and incomplete. Unfortunately, no such dependable varietal history can be written for this crop as for the tomato.

In 1901 American seedsmen listed between 125 and 150 varietal names of peppers in their catalogs. Of this number only 18 to 20 probably denoted really distinct varieties, the others being merely synonyms or cases of misnaming. The history of those varieties, with few exceptions, is indeed obscure. It is noteworthy, however, that after 35 years these distinct sorts are all still available commercially with one or two possible exceptions. Furthermore, there have been few very distinct or very marked improvements in type. Many new names have appeared for old forms, and the old stocks have been improved in uniformity and conformity to type. The principal other improvements made have been in securing somewhat thicker flesh and increased earliness. These improvements have been effected almost entirely by private agencies.

The list of practically all really distinct sorts noted by Tracy (*46, 47*) follows:

Pungent varieties—	Mild varieties—
Bird's Eye	Bellior Bull Nose
Cayenne	Black Nubian
Celestial	Chinese Giant
Cherry	Golden Dawn
Large Red Chili (or Mexican)	Golden Giant
Red Cluster	Monstrous (or Grossum)
Small Chili (Red Chili)	Ruby King
Tabasco	Squash or Tomato
Yellow Cayenne	Sweet Mountain
Yellow Cherry	

Until recently most of the hot varieties were the same as when they were first found by Europeans over 400 years ago. One type, however, has been a subject for improvement since about 1900. The large, long, hot type variously known as a Cayenne or Mexican type, or just as plain Chili, is a very important vegetable in the Southwest. This should not be confused with either the very hot Cayenne variety or the very hot small Chili pepper that is used in making pepper sauce. It is a large elongate sort that is eaten green or ripe and used fresh, canned, or dried.

In 1903 Musser (*14*) introduced Anaheim Chili, named for the town of Anaheim, Calif., an important center of production and drying of this type of pepper. It was developed by mass selection from the Mexican Chili for longer, thicker-fleshed pods. It is still an important variety.

About 1917 Garcia (*16*), of the New Mexico Agricultural Experiment Station, introduced Chili No. 9, also a selection from the native Mexican type. He selected specifically for larger size, thicker flesh, a sloping shoulder to facilitate peeling, productivity, and general adaptability to canning under New Mexico conditions. Incidentally, he obtained an intermediate resistance to fusarium wilt. The strain has replaced most of the older ones grown in the warmer parts of New Mexico.

Recently, by pure-line selection, Miller, of the Louisiana station, has developed a number of highly uniform, intensely colored, productive strains of very hot peppers of the Tabasco and Cayenne types. The production of Tabasco peppers for making Tabasco pepper sauces is an important industry in Louisiana. In 1935 Miller distributed Tabasco 10–1 and Tabasco 10–2. These were developed from the locally grown strains of the variety. Sport was distributed in 1936. It was developed by crossing the local Sport × Honka, an intensely red Japanese variety, then backcrossing to Honka in an effort to further intensify color. A fourth production of Miller's is Selection C–28–11, derived by inbreeding from a locally grown strain, Baton Rouge Cayenne. He selected for superior earliness, greater pungency, yield, and resistance to cercospora leaf spot.

Although the sweet varieties are much more important commercially than the hot varieties, less attention has been given to them by public research agencies in the United States. This is doubtless

because of the keen interest private agencies have shown in the sweet peppers and the very satisfactory contributions they have made.

Two sweet varieties of pepper have been introduced by experiment stations, but so recently that it is impossible now to indicate their probable importance. The Waltham Field Station of the Massachusetts Agricultural Experiment Station introduced Waltham Beauty in 1935. It was selected from an unidentified variety. The Connecticut station introduced Windsor-A in 1936, developed from a hybrid of California Wonder × Bountiful. Both of these new introductions are early, show improved wall thickness, and are adapted to New England conditions.

Practically all of the large-fruited, mild-fleshed varieties were derived by selection or the finding of valuable segregates of natural crosses. The pepper is cross-fertilized to a considerable extent, so that under field conditions natural crosses between varieties may occur frequently. The parent varieties of most of the commercial varieties that have been prominent for the past 50 years are unknown and many of them are relatively old.

As mentioned above, the hot varieties, except for very recent improvements that hardly involve major varietal characters, have been known for 250 to 300 years and even longer. Among the sweet varieties the names of Bell or Bull Nose, Oxheart, and Squash have been current for over 150 years. Most of our present sweet varieties have come from these types. The types were first described about 400 years ago.

Just as the period from 1875 to 1900 was very productive of new introductions and selections of tomato, so it was with peppers. Although many new names and some improved stocks appeared, few really marked advances can be recorded. Many of the supposedly new introductions during that period represented varieties that could be recognized by detailed descriptions in the literature over 200 years old. We may be safe in assuming that nearly all varieties known about 1850 were very old and that about half the "new" varieties introduced between 1875 and 1900 had been known for 100 to 200 years. Table 1 shows only too well the fragmentary nature of our present knowledge of the origin of some of the better known varieties.

There are a few varieties that command special interest. Chinese Giant and Ruby King are doubtless selections out of the old Bell or Bull Nose, and Chinese Giant represents no very great deviation from its supposed parent variety. It is rather late, tends often to be rough, and is only a moderate to shy producer. Ruby King, introduced by Burpee, was a real improvement over the old type, having more attractive, uniform shape, higher productivity, and better quality. The chief claim of Chinese Giant to fame was its size. Ruby Giant and World Beater are two varieties of some importance that were developed from crosses of Chinese Giant and Ruby King. Royal King was selected from Ruby King, and Magnum Dulce, popular for many years, was selected from Chinese Giant. Although the records are incomplete, it appears almost certain that several of the more recent introductions also have been selected from one or the other of these two varieties or from crosses in which one or both were involved. Ruby King is still one of the half dozen most important

sweet varieties and is perhaps more widely grown than any other single variety. California Wonder is considered the most important improvement in many years, on account of its large size, attractive form, uniformity, and very thick, firm flesh. It is rather late, however, and not well adapted to the northern third of the United States. Harris Early Giant, introduced by the Joseph Harris Seed Co., is very popular in the more northerly areas where California Wonder is too late.

TABLE 1.—*Origin of some of the more important pepper varieties of the United States*

Name	Early reference to variety	Varietal history in United States: First described or advertised	Varietal history in United States: Origin
Anaheim Chili		1903	Selected from Mexican Chili by H. J. Musser
Bell (or Bull Nose)	1774	([1])	Precolonial New World
Black Nubian	1733	1991	European variety
California Wonder		1828[2]	Selection by a California grower
Cardinal		1887	
Cayenne	1542	([1])	Supposedly French Guiana
Celestial	1731	1887	Chinese variety
Cherry	1586	([1])	Precolonial New World
Chilli (or Chili)	1588	([1])	Do
Chinese Giant		1900[2]	Selection from Bell (?)
Elephant's Trunk		1892	Selection from Cayenne (?
Etna	1640	1890	First advertised by W. Atlee Burpee & Co
Golden Dawn		1882	
Golden Neapolitan		1906	Chance seedling in Neapolitan
Golden Upright		1887	Unknown
Harris Earliest		1920	Introduced by Joseph Harris Seed Co
Kaleidoscope	1632	1890	Precolonial New World
Long Red	1813	([1])	Do
Long Yellow Cayenne	1832	([1])	Do
Magnum Dulce		1904	Selected from Chinese Giant
Monstrous		1867	Selected from Bell (?)
Neapolitan		1903	Italian variety
Nepal Chili	1809	1895	
New Mexico Chili No 9		1917	Selected from Mexican Chili by F. Garcia
Oxheart		1844	
Perfection		1912	Selected from Spanish pimiento by S. D. Riegel
Royal King		1918[2]	Selected from Ruby King by George Riegel
Ruby Giant		1906	Ruby King × Chinese Giant
Ruby King		1884	First listed by W. Atlee Burpee & Co
Squash (or Tomato)	1686	([1])	Precolonial New World
Sunnybrook		1922	Selected from Squash. Introduced by W. Atlee Burpee & Co
Sweet Mountain		1849	Selected from Bell (?)
Tabasco	1888	([1])	Introduced from Mexico
Waltham Beauty		1935	Selection
World Beater		1919	Chinese Giant × Ruby King

[1] Unknown, very old. [2] Approximate date.

The sweet peppers of the Squash or Tomato type are very popular for home garden and local market use, but are relatively unimportant in the heavy commercial shipments. Sunnybrook, introduced by Burpee, is the best known and most important of these. A tempest raged a few years ago in the horticultural press over claims that certain varieties of this group represented hybrids between pepper and tomato. The new names involved in the controversy implied hybrid origin, and the varieties were advertised and sold with the claim that they were new hybrids. However, numerous botanists, horticulturists, and growers who know peppers and tomatoes have never been able to detect any trace of tomato characteristics in either the plant or the fruit. The tomato shape proves nothing, for that

has been known in peppers for about 400 years. Furthermore, tomato and pepper belong to such distantly related genera that crossing the two is believed to be impossible. There is, at least, no convincingly documented case of such a hybrid known, despite the fact that skillful workers have often tried to cross them.

Another interesting varietal development is that of the Perfection pimiento pepper, selected to meet a specific requirement by S. D. Riegel, of Georgia. The introducer of this variety was engaged in the canning of peppers and required a very mild, very thick-fleshed sort having specific qualities of flavor and adaptability to canning. Since no such variety was grown in the United States at that time, he obtained seed of a Spanish pimiento from Spain. The variety name was not stated, but it was probably Sweet Genua or a closely related form. From this Spanish stock a single plant was selected having the desired characters and apparent adaptability to conditions in the southern United States. The variety Perfection was developed by selection from the progeny of this plant and first introduced to the trade about 1912.

EGGPLANT

History

THE eggplant, *Solanum melongena* L., is believed to be native to the Tropics of the Old World. It was referred to in Chinese writings of some 1,500 years ago, and by various early writers in the sixth, ninth, twelfth, and thirteenth centuries (*18*). It appears to have been unknown in Europe in ancient times and is therefore believed to be Asiatic in origin. Vavilov (*48*) has concluded through his botanical-geographic studies that there were two centers of origin, the first in subtropical or tropical India, the second in China.

In the sixteenth century various writers described eggplants of the several colors known today—purple, yellow, white, ash-colored, green, and brownish. The oblong or elongated, pear-shaped, and round forms were also known in that early day. At present there is almost no interest in any but the purple-fruited sorts in the United States, but occasionally other colors are grown for ornament. There is good evidence that no new or distinct types have been developed within historic time, although of course numerous variations or varieties have been found and propagated within each type. It is probable that considerable increase in size has resulted from comparatively modern efforts, because the varieties described early in the seventeenth century seem to have been rather small. A hundred years later descriptions are found indicating fruit sizes that are comparable with our present sorts.

Vilmorin-Andrieux & Cie., Paris (*49*), in 1856 described 7 varieties, including Long Purple, Round Purple, Chinese Long White, Large Purple, and Guadaloupe Striped. Burr (*5*), in this country, in 1865 listed these same varieties as of interest here, and in addition described New York Improved. New York Improved and Long Purple are still among the half-dozen varieties of commercial importance in the United States today.

The eggplant does not have any great appeal to the majority of consumers in this country, so it remains a minor crop—and probably will

so remain for a long time. This general lack of interest is reflected in the small attention it has received here from plant breeders and investigators. There are few varieties grown in the United States, and little is being done to produce new ones. In the Orient, however, the situation is quite different. The eggplant is one of the most important vegetables in China, Japan, and India, holding in those countries a position more nearly comparable with that of the tomato in North America. Because of its extensive use and popularity in the Orient, numerous varieties have been developed and it has been the object of perhaps more genetic and cytological study than in Europe or North America. Numerous oriental varieties have been introduced for trial by American growers and seedsmen but have never attracted interest. Some of them are quite productive, but generally they are of small-fruited types or of colors that do not appeal to us.

Breeding and Improvement

All our important commercial varieties are the result of work by private gardeners and seedsmen. Most of them were doubtless obtained merely by selection from the old long-established types and represent minor improvements except in fruit size and uniformity. Unfortunately we are unable to determine with certainty the time, manner, and place of origin of our present varieties.

The white, striped, and scarlet-fruited sorts are all very old and are of interest only as novelties or ornaments, so they will not be discussed here.

Of the purple-fruited sorts, Round Purple and Long Purple doubtless were imported from Europe a century or more ago. Vilmorin-Andrieux & Cie. (*49*) lists Large Purple as of American origin, introduced in 1854. The parentage is unknown.

Burr (*5*) lists New York Improved, indicating that it was derived from Large Round. It was described as having spiny leaves. It appears that the variety was developed by selection about 1850 by Brill, a gardener and seed grower of Long Island, N. Y., and named by him. The modern strains of New York Improved are spineless. Spineless strains have been available since about 1900.

Black Pekin was a popular variety for many years but is now rarely listed. It was introduced from China about 1870.

Black Beauty appeared about 1900. It is said to have been originated by Ashcraft, a gardener and seed grower of Swedesboro, N. J. There is little question that Black Beauty has been the most popular eggplant variety grown in the United States. The intensely dark-purple, or purplish-black, fruits of medium-large size are very attractive and are largely responsible for its outstanding prominence.

The old Long Purple variety has been the subject of selection for earliness, particularly in the Northern States. Early Long Purple, or simply Long Purple, is the earliest variety commonly grown, but is grown extensively only where earliness is essential.

The most important development since Black Beauty is the Florida High Bush. It was introduced about 1905 by a Florida grower who selected it for its tall upright growth and habit of bearing its fruits well up off the ground. This character is often of considerable im-

portance as an aid in avoiding losses from fruit rots or other damage resulting from contact with the soil.

The agricultural experiment stations of New Hampshire, Rhode Island, and Wisconsin are all working for increased earliness in eggplant to permit its being grown profitably farther north. The Central Experimental Farm of Canada, at Ottawa, has introduced Blackie, a selection smaller and earlier than Black Beauty that is also more productive in the North.

Kakizaki (*25*), in Japan, demonstrated the commercial feasibility of artificially produced hybrid eggplant from inbreds known to be superior for the purpose. In 1931 he introduced Black Bountiful, a first-generation hybrid which has been offered for sale in the United States by Japanese seedsmen. It is distinctly smaller than our well-established sorts and so has not become popular here. However, it is early and very productive.

STUDIES OF INHERITANCE AND CYTOLOGY IN SOLANACEOUS FRUITS[5]

Tomato

The first investigators (*17*, *41*) of the mode of inheritance of specific characters in the tomato quite naturally and logically examined certain of the most obvious features of plant and fruit, such as cotyledon size and shape, leaflet size and shape, leaflet surface character, plant stature, growth habit, fruit color, fruit shape, and internal structure of fruits. Such studies have been made over the last 30 years, but the most conclusive results have been reported in the last 15 years. J. W. MacArthur, at the University of Toronto, and E. W. Lindstrom, at the Iowa Agricultural Experiment Station, are the most active in studying inheritance in "normal" individuals, while J. W. Lesley and M. M. Lesley in California, F. W. Sansome in England, besides Lindstrom, are engaged with cytological studies, induced mutations, polyploidy, and the occurrence of aberrant forms.

A large number of workers have contributed to the present knowledge of inheritance of specific characters in the tomato, but it is not necessary to cite here all the literature of all workers. Table 2 presents a summary of the characters studied to date, with data concerning dominance and indications as to whether the contrasted characters are due to differences in one or more factors. Most of those listed represent single factor differences.

Unfortunately, the characters that we most desire to incorporate into our new varieties to meet new needs cannot be listed in the table at this time. These are resistance to specific diseases, such as fusarium wilt, verticillium wilt, nailhead, leaf mold, septoria, mosaic, streak, and curly top. Although there are many varieties showing a fairly high resistance to fusarium, a few resistant to nailhead, and resistance to leaf mold, nothing certain is known about the number of factors involved in resistance to any of these diseases, and there are only general unconfirmed indications of the dominance or recessiveness of resistance.

[5] This section is written primarily for students or others professionally interested in breeding or genetics.

TABLE 2.—*Inheritance in the tomato*

Characters	Genes	Behavior in F_1	Segregation in F_2	Authority	Tetraploid segregation (after Sansome, *44*)
Flesh color					
Red *v* yellow	*R r*	Red	3 red to 1 yellow	(*17, 29 34 37 41*)	Between 22 1 and 35 1
Red *v* tangerine orange	*T t*	do	3 red to 1 tangerine orange	(*3 37*)	
Skin					
Yellow *v* colorless	*Y y*	Yellow	3 yellow to 1 colorless	(*17, 29 34, 37 41*)	Approximately 35 1
Dark green base *v* uniform green fruit	*U u*	Dark green base	3 dark green to 1 uniform	(*37*)	Approximately 22 1
Smooth *v* pubescent	*P p*	Smooth	3 smooth to 1 pubescent	(*17, 29, 34 37*)	
Shape of fruit					
Globe *v* pear		Globe	Gradations Tend toward 3 1	(*34 3*)	
Short *v* elongated	*O o*	Short	3 short to 1 elongated	*29,*	
Normal *v* fasciated	*F f*	Normal	3 normal to 1 fasciated	*34 3*	
Normal *v* nipple tipped	*N n*	do	3 normal to 1 nipple tipped	(*34 3*	
Locules in fruit					
2 locules *v* many		2 locules	Approximately 3 1	(	
Size of fruit					
Large *v* small		Intermediate	All gradations	(*29, 30 3 37 41*	
Plant habit					
Tall *v* dwarf	*D d*	Tall	3 tall to 1 dwarf	(*17, 29, 37 41*)	Approximately 22 1
Dwarf *v* extreme dwarf	*D d*	Dwarf	3 dwarf to 1 extreme dwarf	*34 37*)	
Tall *v* brachytic	*B_r b_r*	Tall	3 tall to 1 brachytic	(*34 37*	
Normal *v* self topping	*Sp sp*	Normal	3 normal to 1 self topping		
Leaves					
Green *v* yellow color	*L l*	Green	3 green to 1 yellow lutescent	(*1)*	
Normal *v* potato leaf	*C c*	Normal	3 normal to 1 potato leaf	(*17, 41*)	
Normal *v* wiry	*W w*	do	3 normal to 1 wiry	*34*	
Normal *v* wilty	*W_i w_i*	do	3 normal to 1 wilty	(*34, 37*	
Normal *v* hurle	*H h*	do	1 normal 2 intermediate 1 hurle	*3*	
Inflorescence					
Simple *v* complex	*S s*	Simple	3 simple to 1 complex	*34*	Approximately 22 1
Normal *v* leafy	*Lf lf*	Normal	3 normal to 1 leafy	(*34 37*	
Stem color					
Purple *v* green	*A a*	Purple	3 purple to 1 green	(*34 37*	
Purple *v* becoming green	*A a_2*	do	3 purple to 1 becoming green	*34 37*)	
Time of maturity					
Early *v* late		Intermediate	All gradations	( )	
Pedicel					
Jointed *v* nonjointed	*J j*	Jointed	3 jointed to 1 nonjointed	(	
Hereditary radium induced mutations of Lindstrom [1]					
Leaves					
Normal *v* rough	*R_1 r_1*				
Normal *v* yellow	*L l*				
Cotyledons					
Normal *v* rolled	*R_c–r_c*				
Sterility					
Normal *v* sterile	*S_r–s_r*				
Seedlings					
Normal *v* yellow (lethal)	*Y_s y_s*				
Normal *v* virescent white	*V–v*				

[1] All 6 characters monorecessives, *l* shown to be same character previously known (*32*)

Several difficulties have stood in the way of acquiring this much-needed information. First, strong resistance to certain of these diseases is at present unknown in any form of tomato. Wide search has yielded no appreciable resistance to mosaic, streak, or curly top. And in those cases where a degree of resistance is known, it is usually such an intermediate or partial resistance that it cannot be measured with any dependability. Until methods are developed that will permit accurate determination of the amount of resistance in a plant, under even a single set of reasonably standardized experimental conditions, progress will necessarily be slow. It must be possible to repeat tests with given stocks and get results that will consistently agree if we are to know much about resistance.

Another difficulty is space requirement and cost of conducting such tests with the tomato. Thousands of small-grain plants or peas can be tested on a few square rods of land or a few benches in the greenhouse; but in the field, 15 to 20 square feet is needed for each tomato plant, and 3 to 4 square feet of precious space in the greenhouse. The worker with small plants can test thousands or hundreds of lines where the tomato investigator can handle only hundreds or dozens.

There also has been too much pressure for quick practical results, and many workers have felt it necessary to hurry without being able to make the desirable and often essential preparatory surveys and studies. Now a number of research agencies are backing up for a new start, but they are first carefully preparing to ferret out essential basic information before launching further into practical application of research. It is hardly possible to apply what isn't known.

In his quest for leaf-mold resistance, Alexander (*1*), at the Ohio station, has isolated apparently homozygous resistant lines from segregating progenies of a cross between an off-type resistant plant and the variety Marhio. The off-type plant bore very small fruits on simple inflorescences and appeared to be from a chance cross with the Red Currant variety. Von Sengbush and Loschakowa-Hasenbusch (*45*) have reported that *Solanum racemigerum* Lange (known in the United States as *Lycopersicon pimpinellifolium* Mill.) is completely resistant to leaf mold and that resistance in this species is due to a single dominant factor. They have also reported a recessive form of resistance in the variety Stirling Castle. Alexander's data, although admittedly meager and not taken as part of a genetic study, also indicate a recessive resistance in Stirling Castle and a dominant resistance in Satisfaction, another English greenhouse sort.

D. R. Porter, at the California station, has noted appreciable resistance in *L. pimpinellifolium* to western yellow blight, a virus disease, and is attempting through crossing and backcrossing to incorporate the resistance rapidly into acceptable commercial types. He is also studying the genetics of resistance.

Porte and Wellman, of the Bureau of Plant Industry, found one line of *Lycopersicon pimpinellifolium*, when grown in heavily artificially infected fusarium wilt soil, to be practically immune to wilt and highly resistant to a number of leaf diseases. They used a technique similar to Porter's in order to transfer higher degrees of fusarium resistance to commercial sorts than they commonly carry. By controlled pollination they have also developed a large number of inbred lines of

commercial varieties resistant and susceptible in all degrees. This was preparatory to determining the nature of such disease resistance as the lines possessed, which might be used in further breeding. It has not been possible to observe consistent percentages of resistant and susceptible individuals in repeated tests of a stock or line, or consistent degrees of injury to the plants in repeated inoculation tests. The effects of the texture, moisture, hydrogen-ion concentration, soluble salts, temperature, and fusarium content of the soil, the temperature and humidity of the air, the effect of light, age, and size of plant, and other such factors upon infection and reaction of the plant to the parasite are almost if not entirely unknown. These must be learned and test conditions properly standardized before dependable comparisons of resistance can be made. Special studies are, therefore, in progress in efforts to perfect a technique for dealing with the incomplete type of fusarium resistance, the only type definitely reported to date.

C. M. Tucker, at the Missouri station, has recently reported to the writer that among many seed lots of *Lycopersicon pimpinellifolium* tested, one appears to possess complete dominant resistance to fusarium wilt. Other lots either were 100-percent susceptible or showed the intermediate resistance that is typical of resistant commercial varieties. At this writing his studies have not proceeded far enough to determine more.

A number of other investigators are busy with disease resistance and with selection for improved adaptation to specific requirements, but reports are not now available as a basis for discussing their work. (See list of projects and workers in the Appendix.)

Wellington (*51*) reported yields of F_1 intervarietal hybrid tomatoes about 21 percent higher than the yields of the more productive parent, 45 percent higher than the mean of the two parents, and 71 percent higher than the lower yielding parent.

Linkage in the Tomato

Thus far, the chromosome map of the tomato hardly has its outlines well drawn. MacArthur (*34, 35, 36, 37*) and Lindstrom (*29, 30, 33*) have made the major contributions to knowledge of this problem. Of some 20 genes that are known, the positions of 16 have been located on 10 of the 12 pairs of chromosomes. Six of the groups now contain two or more known genes.

The chromosome map showing the linkage groups and the probable order of the genes within the groups may be represented roughly as follows:

Chromosome	Genes	Chromosome	Genes
I	D_1-*P*-*O* *S* (and genes for earliness ?).	VI	*L* (and genes for earliness and size ?).
II	*R* (?).	VII	*U*-*H*-*T*.
III	B_r-*Y*.	VIII	A_2 (?).
IV	*C*-S_p.	IX	D_2 (?).
V	*F*-A_1-L_f-*J*.	X	W_t *N*.

The second, sixth, eighth, and ninth chromosomes each bear but one known factor.

Currence (*7*) has recently pointed out a relation between genes of the D_1POS region of the first chromosome and genes affecting earliness. The actual nature of the factors involved has not been determined, but *D* and *DP* lines were, on the average, 9 and 14 days earlier respectively than corresponding *d* and *dp* progenies.

MacArthur (*36*) has also recently added evidence of a possible linkage of genes for earliness and size—if there are such—with certain qualitative factors. He showed that *l*, a recessive gene for yellow-green foliage, retards maturity about 2 weeks and reduces fruit size 30 percent. The author recognized that the existence of size and earliness genes linked with *l* was not demonstrated, for the effect might possibly be due directly to *l* or other genes. It is logical to suppose that *l* would have a marked direct effect on plant and fruit development.

It is unfortunate that we do not yet have accurate information regarding inheritance of disease resistance and possible linkages with qualitative genes. Some observations might lead us to suppose that at least certain types of resistance are linked closely with specific characters.

Cytology of the Tomato

Thus far very little if any attention has been given to the cytology of hybrids of *Lycopersicon esculentum* Mill. and related species. The large number of small chromosomes make cytological study quite difficult. In the intensive drive for disease resistance, however, it seems sure that wider and wider crosses will be attempted, with the failures, sterilities, and various aberrations that accompany such efforts. Workers will then find it necessary to study both the normal and the abnormal material cytologically more than has been done in the past.

Most of the cytological work done on the tomato has been in the study of triploids, trisomics, and both natural and artificially induced tetraploids. All three of these chromosomal aberrations occur rather frequently in cultivated fields and may become evident through the departure of the plant from the typical vegetative form and fruitfulness of the variety in which the aberrations appear. A number of these have been described in detail by Lesley (*26*, *27*), Lindstrom (*31*), and others. In general the plants are characterized by a sturdier, stockier appearance; thicker, more rugose leaves; and little or no fruit. They generally produce a large proportion of abortive pollen and may be unfruitful for that reason if not for others.

The normal n number of chromosomes in the tomato is 12, and the $2n$ or somatic number is 24. Aberrant plants have been found with 25, 26, 27 (aneuploids), 36 (triploids), and 48 (tetraploids) somatic chromosomes, and also some with fragments of additional chromosomes. Lesley (*27*) has obtained 12 different simple trisomics, each with a different supernumerary chromosome, by crossing a triploid ($2n=36$) plant with a normal diploid ($2n=24$). He has identified these as Triplo-A, Triplo-B, Triplo-C, etc., depending on which one of the 12 chromosomes occurred as a supernumerary. These identifications of extra chromosomes and the determinations of trisomic ratios in the progenies of hybrid trisomics have afforded additional confirmation of the connection between genes and chromosomes and may add

to knowledge of linkage relations. An understanding of what is happening to the chromosomes of these aberrant plants helps to make it clear why they will not breed true and why it is so difficult, if not impossible, to make practical use of certain desirable characters that some of them have.

Several workers—Winkler (*52*), Jørgensen (*23*), Sansome (*44*), and others—in addition to those already named have induced the formation of tetraploids by cutting off stems of plants. Callus tissue rapidly forms under proper conditions, and in this tissue cells are occasionally formed with 48 instead of 24 chromosomes. Some of these cells may develop into shoots and continue growth in a more or less normal manner. Since these tetraploids are usually nearly sterile or quite so, and since they do not breed true, they are usually propagated vegetatively for experimental purposes. Thus far there is no proved case of a commercially valuable tetraploid.

Lindstrom (*31*) has reported a highly fertile tetraploid of *Lycopersicon pimpinellifolium* obtained from callus tissue, but it is apparently the only such case noted. Some are inclined to believe that the parent plant was not homozygous but that *L. esculentum* was involved. The tetraploid was cross-sterile with the parent type.

A variation with less than the normal number of chromosomes has also been observed. Lindstrom has described a haploid tomato (12 somatic chromosomes as well as 12 in the germ cells). It was found in the F_2 of a varietal cross of completely fertile varieties. The haploid was smaller than normal and almost completely sterile. Its pollen was apparently impotent and few seeds were borne when other pollen was applied to its flowers. There was no tendency to pairing of the chromosomes, but evidence of a tendency toward reduction or separation in the meiotic division. It appeared that any germ cell receiving less than 12 chromosomes aborted.

A few diploid cells were noted in roots, so the plant was carefully perpetuated by cuttings in the hope that doubling might occur in a cell destined to become a growing tip and thus give rise to an absolutely homozygous tomato. Not only diploid but tetraploid plants were finally obtained.

Lesley and Lesley (*28*) have obtained tomato plants bearing fragments of single chromosomes by crossing a double trisomic ($2n+1+1$ chromosomes) with a normal plant. Certain of the progenies of this cross variously contained $2n+1$, $2n+1+$a fragment or $2n+$a fragment. These fragments or incomplete supernumerary chromosomes represent a partial trisomic condition. Such plants resemble certain trisomics. It has been found that fragmentation occurs in those unpaired chromosomes that lag behind in the course of meiosis.

The results of chromosome injury or of "knocking out" factors from chromosomes by irradiation may well be considered at this point. Lindstrom (*32*) irradiated various portions of tomato plants with radium-bearing needles. Irradiation of growing tips induced the most variations in the progeny of the treated plants. The irradiated parent plants showed no sudden variation except what could be accounted for as a result of direct injury by the radium in cases of overdosage. The progeny of these plants, however, showed much sterility,

pollen abortion, and malformation, supposedly caused by chromosome damage.

From these progenies Lindstrom isolated six variations that bred true and were shown to be due in each case to a single recessive factor. Five of these never before had been observed in tomato, while *l* for yellow foliage was shown to be the same factor that had been known for many years (table 1).

MacArthur (*38*) accomplished somewhat similar results by irradiating seeds with X-rays. All plants and fruits from these seeds were normal, but their progeny showed 12.4 percent of mutants of diverse forms—all of them economically worthless. There were many lethals and semilethals among them, only about a dozen being capable of perpetuation in the homozygous condition. Most of the variations appeared as chlorophyll and leaf abnormalities, and the plants were very slow-growing. Most of the new characters susceptible of genetic study, as in Lindstrom's radium-induced variations, behaved as single recessive factors.

Pepper

The principal contributions to the knowledge of inheritance in the pepper have been made by Halsted (*17*), Webber (*50*), and Dale (*8, 9, 10*) in this country, Ikeno (*20, 21*) in Japan, Atkins and Sherrard (*2*) in England, and Deshpande (*11*) in India. These workers are in general agreement on the inheritance of a number of characters but disagree on others. In cases of disagreement it appears that the more recent workers are probably more nearly correct because they have generally used larger progenies and have studied the results in F_3 and backcross generations as well as in the F_1 and F_2 generations. In some of the earlier work the importance of environment in its effect on expression of specific characters was not fully appreciated and difficulties were encountered. In table 3 are presented data on the inheritance of 16 characters in pepper. Conflicting data are not presented, but only those believed to be most dependable as indicated by the respective experimental procedures.

All investigators of foliage and flower color agree on the dominance of purple *A* over nonpurple *a* and on the close linkage or identity of factors responsible for foliage and flower color. Deshpande (*11*), however, only recently pointed out the effect of a second factor for purple foliage, an intensifier, *B*, which is without effect when *A* is absent. Numerous workers agree that red color of the ripe fruit is dominant over yellow and that green color of the immature fruit is dominant over yellow. Each is due to a single factor. Again Deshpande (*11*) contributed new information when he showed the effect of *A* upon fruit color. Plants with purplish-red fruit crossed with pure yellow gave four color types in a typical dihybrid 9:3:3:1 ratio in the F_2, namely, purplish red, pure red, yellow overcast with purple, and pure yellow. He also pointed out a close association between fruit color and seed color. Red fruits bear reddish-yellow seeds, while yellow fruits bear light or pale yellowish seeds.

Dale (*8*) plotted size distribution curves of pod lengths of F_1 and F_2 progenies of Coral Gem × Anaheim Chili (short × long pod) and certain backcrosses. The curves were skewed when plotted against class intervals of equal arithmetical magnitude, but were normal when plotted

on a logarithmic basis. It was concluded that the several undetermined factors for pod length exerted proportionate rather than additive effects, and that there was no disturbing influence of dominance.

TABLE 3.—*Inheritance in the pepper* (*Capsicum annuum*)

Characters [1]	Genes	Behavior in F_1	Segregation in F_2	Investigators
Plant habit:				
Normal *v.* dwarf		Normal	3 normal to 1 dwarf	Dale (*10*).
Flower color:				
Violet *v.* white		Intermediate violet	3 violet to 1 white	Ikeno (*20*), Deshpande (*11*).
Foliage and stem color: [2]				
Purple *v.* nonpurple	*A a*	Intermediate purple	3 purple to 1 nonpurple	Deshpande (*11*).
Intense *v.* normal purple	*B b*	Intermediate purple (intensifier only).	Together with *A* gives 1:3:8:4, three grades purple, 1 nonpurple.	Do.
Fruit color: [3]				
Red *v.* yellow or orange	*R-r*	Red	3 red to 1 yellow or orange.	Several.
Green *v.* yellow (immature).		Green	3 green to 1 yellow	Webber (*50*), Deshpande (*11*).
Fruit shape:				
Blunt *v.* nonblunt apex	*D-d*	Intermediate	3 not blunt to 1 blunt	Deshpande (*11*).
Bulged *v.* nonbulged base.	*F-f*	Bulged	3 bulged to 1 nonbulged	Do.
Fruit position:				
Pendent *v.* erect	*P-p*	Mostly pendent	3 pendent to 1 erect	Deshpande (*11*), Kaiser (*24*).
Fruit calyx: [4]				
Nonclasping *v.* clasping	*E-e*	Nonclasping	3 nonclasping to 1 clasping.	Deshpande (*11*).
Fruit flavor:				
Pungent *v.* mild		Pungent	3 pungent to 1 mild	Webber (*50*).
Fruit size and shape:				
Large *v.* small		Intermediate	All grades.	Several.
Elongate *v.* globose		do	Many grades; 3 factors indicated.	Deshpande (*11*).
Pedicel length:				
Short *v.* long		Short	3 short to 1 long	Do.
Pubescent foliage:				
Pubescent *v.* glabrous		Intermediate	15 pubescent to 1 glabrous.	Ikeno (*20*).
Inflorescence:				
Nonumbel *v.* umbel		Nonumbel	3 nonumbel to 1 umbel	Do.

[1] Hybrid vigor pronounced in plant vigor, height, yield, increased earliness, and fruit diameter (Deshpande (*11*). Length of pedicel, petal, and fruit linked with plant color and fruit position; these in turn linked with fruit color. All these factors on 1 chromosome (Deshpande (*11*)).
[2] Purple of stems and foliage closely linked with flower color; *A* affects fruit color, giving typical dihybrid ratio 9:3:3:1 in F_2.
[3] Seed color closely linked with flesh color.
[4] Nonclasping calyx closely linked with bulged base; 3 percent cross-over.

Branching habit, leaf size, and fruit size were shown by Webber (*50*) and others to be controlled by several factors, as evidenced by the intermediate character of the F_1 and the occurrence of all gradations of habit or size in the F_2.

Kaiser (*24*) showed the hereditary position of the fruit (pendent *v.* erect) to be due to a response to geotropic stimulus rather than orientation with reference to the plant axis or branch. A single dominant factor is responsible for the pendent position.

Dale (*10*) studied a leaf variegation in the pepper, which he found to be inherited maternally. Ikeno (*21*) observed other variegated forms in which the variegation was transmitted by either male or female gamete. Selfing of these races yielded only variegated offspring. Crossing variegated with green resulted in dilution of the variegated character. Cytoplasmic transmission is thought to have

been involved in both these instances. Other workers dealing with other plants have reported many cases of apparently cytoplasmic inheritance, particularly in cases of leaf variegation.

With one exception, all reports on the chromosome number of pepper are in agreement. Kostow, according to Huskins and La-Cour (*19*), reported a haploid number of 6 for *Capsicum annuum*, but later workers have consistently reported 12. Huskins and La-Cour (*19*) studied a dozen varieties among three subspecies and found only normal figures of 12 chromosomes in the haploid and 24 in the diploid states. Dixit's (*12*) results agreed with these.

No such interesting observations of polyploidy have been made in pepper as in tomato. It can hardly be said that polyploidy does not occur in pepper, but a search of recent literature failed to reveal record of studies of polyploids or chromosomal aberrations in this plant. Cases will come to light as the cytologist turns more attention to it, no doubt, for the family Solanaceae is one of the most productive of these types of variation.

Eggplant

As mentioned above, the eggplant has been studied very little from the cytogenetic standpoint, and most of the work done has been by other than United States investigators.

Halsted, of New Jersey (*17*), Nolla (*39*), of Puerto Rico, studying at Cornell University, and Kakizaki, in Japan (*25*), have studied the inheritance of color.

Halsted found two pairs of genes for fruit color. Purple skin *v.* colorless skin is due to a single dominant gene, as is also green flesh *v.* white flesh. He obtained four color types– *PG* purple (purple skin, green flesh), *Pg* pink (purple skin, white flesh), *pG* green (colorless skin, green flesh), and *pg* white (colorless skin, white flesh). He also studied a variegated fruit color that he found to be recessive.

Nolla confirmed Halsted's studies on fruit color and extended his observations to leaf and stem color, corolla color, and a striping of the anther. He found purple color in vegetative and floral parts to be either very closely linked with fruit color and with each other or controlled by the same gene. Without exception fruits with purple skins were borne on plants with violet or purple corollas and purple-tinged foliage. Green-fruit forms were borne on pure green plants with white corollas. Violet or purple corolla *v.* white was due to a single dominant factor, as was striping *v.* nonstriping of the anther. Monohybrid ratios in close conformity to the theoretical were obtained in the F_2 for all these characters.

In his studies of hybrid vigor in eggplant, Kakizaki (*25*) determined the seed and fruit weights, stem diameters, and heights of some 30 intervarietal crosses. He also recorded the F_1 behavior with reference to branching habit, leaflet size, fruit shape, color, and occurrence of calyx spines.

In the F_1 generation branching, leaflet size, fruit shape, and calyx spines were intermediate between the parents. Purple skin was dominant over white.

The mean seed weight of 30 crosses was 18 percent heavier than that of the mother parents. These results were generally consistent in 3

successive years, and were compared with selfed maternal parent seeds grown in the respective years.

The F_1 plants showed a mean stem diameter and height increase of 6 percent over the mean of the parents, and 36 percent increase in yield. The F_1 progenies were 70 percent more productive than the lower yielding parent and 17 percent more than the higher yielding parent. The best two parents for crossing gave F_1 progenies 90 percent more productive than the standard. Other Japanese workers have also noted marked hybrid vigor in eggplant. This work led to the commercial production of hybrid seed mentioned above.

It does not follow, however, that all intervarietal crosses will prove to be subsequently productive in all respects. Rao Balaji (*43*) has noted a high degree of partial sterility in the F_1 plants of certain wide crosses of Indian varieties. The pollen was 90 to 95 percent abortive.

Yasuda (*53*) has induced the formation of fair-sized parthenocarpic eggplant fruits by pollinating the flowers with petunia pollen. Cytological study showed that the petunia pollen tubes never reached the micropyle of the eggplant ovule, indicating that the stimulus of pollination alone induced ovary development. Injections of an extract of petunia pollen into ovarian tissue of the eggplant produced a similar effect, but tomato pollen extract was less effective.

The haploid chromosome number of eggplant is 12, the diploid 24. A few cases of polyploidy have been observed, but thus far none has any economic value. Janaki Ammal (*22*) found a tetraploid in a field culture that was nearly barren. Among the progeny of this tetraploid, triploids (36 chromosomes), tetraploids (48), and aneuploids of 44 to 46 chromosomes were found. He concluded that the triploids arose from a diploid pollen grain. Selfing of one of the triploids yielded 14 seeds, which produced 13 living plants. Of these, 2 were tetraploids and 11 were near-tetraploids, the counts of which could not all be determined with certainty. All these plants with aberrant chromosome numbers were decidedly undesirable from an economic standpoint and were almost entirely sterile.

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BREEDING AND IMPROVEMENT OF CUCURBITS

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THE cucurbits—cucumbers, muskmelons, watermelons, pumpkins, and squash—belong to the family Cucurbitaceae. Botanically they form rather a homogeneous group. While they are extremely diverse in fruit and vine characteristics, their floral structures are in many respects very similar.

In general, the family is characterized by the flowering habit known as monoecious. A monoecious species or variety is one that bears its pistillate or female organs of reproduction and its staminate or male organs in separate flowers, both kinds of flowers occurring on the same plant. In the Cucurbitaceae the female and male flowers are easily distinguished, even before they open. The showy corolla, or petals, of the pistillate flower is attached to the end of an easily recognizable, small, undeveloped cucumber, squash, or melon as the case may be (fig. 1, *A*). The male flower is at the end of an ordinary flower stem, without any enlargement (fig. 1, *B*). The corolla surrounds the pistils or the stamens in the respective sexes.

Cucumber, squash, and pumpkin are normally strictly monoecious, but certain varieties of muskmelon and watermelon show a modification of this condition that is termed andromonoecious. An andromonoecious plant is one that bears bisexual or complete flowers, instead of strictly pistillate ones, in addition to purely staminate flowers.

Although at a cursory glance these bisexual, complete, or hermaphrodite flowers appear like ordinary pistillates, examination within the corolla will show the presence not only of the stigmas but of functional stamens as well. Such flowers can be self-fertilized by their own pollen, or by the pollen from a purely staminate flower or from another complete flower on the same plant.

Our knowledge of the genetics of the cucurbits is very meager and fragmentary. There are several reasons for this. Probably the most important one is economic. The plants are large, and the space required to produce the numbers demanded for statistical significance in genetic experiments is enormous. Recently, however, promising results from systematic breeding programs with melons, watermelons, and squash have enriched our knowledge of the fundamental genetic nature of these crops (*13*),[1] and this in turn should be useful in further breeding work.

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[1] Italic numbers in parentheses refer to Literature Cited, p. 231

Figure 1.—Squash blossoms, structurally typical of the cucurbits: *A*, pistillate flower showing undeveloped fruit to which the corolla is attached; *B*, staminate or male flower.

BREEDING RESPONSES AND POLLINATION TECHNIQUE

Studies made by numerous investigators of the cultivated cucurbits show that the several species are alike in certain breeding responses and variations in reproductive behavior. These points may well be treated here, since they seem to apply to the several crops.

Haber (*8*), working with Des Moines squash, a trailing variety of *Cucurbita pepo* L.; Scott (*25*) with three bush types of *C. pepo* (White Bush Scallop, Giant Summer Crookneck, and Zucchini), and also (*23*) with muskmelon; Porter (*18*) with watermelon; Cummings and Jenkins (*3*), with Hubbard squash, a variety of *C. maxima* Duchesne; and other investigators have shown that loss of vigor does not necessarily follow as a result of inbreeding these plants. This is quite contrary to the usual situation with normally cross-bred plants. Scott and Porter have shown that inbred lines having greater, equal, and less vigor or size of fruit may all be isolated from a given individual and that no difficulty may be expected from self-sterility in such inbreds. The work of Rosa (*21*), of Scott (*25*), and of Porter (*18*)

indicates that hybrid vigor does not occur as a result of crossing inbreds—also contrary to what might be expected.

Rosa (*20*) has sought evidence of metaxenia in muskmelon and Hibbard (*9*) in squash, but no such phenomenon was observed in either case. Metaxenia here refers to an immediate effect of pollen upon the character of the fruit or gross seed characters.

The constancy of these results for a wide range of varieties among several species of the cucurbits is rather conclusive evidence against the loss of vigor from inbreeding or the occurrence of hybrid vigor or of metaxenia in any of the cucurbits discussed in this article.

Another characteristic common to cucumber, squash, muskmelon, and certain other cucurbits is the wide variation within varieties in the ratio of male and female flowers. This ratio is profoundly influenced in many varieties of cucumber by changes in season (length of day) and in nutrients (*5*, *29*); and in squash by season and load of developing fruits borne by the plant (*24*). Under certain unfavorable conditions some varieties may become almost monosexual (all pistillate or all staminate), so that the investigator has great trouble in obtaining the desired set of fruit and seed.

Whitaker (*32*) has published a brief review of the literature on this subject, together with data on the typical sex expression of 49 varieties of cucurbits in 8 species and 4 genera and on deviations from typical expression in each species. His data showed very wide fluctuations in the ratio of male to female flowers in the several varieties and species. He concluded that sex determination in these cucurbits appeared to conform to Correns' theory as applied to monoecious flowering plants. According to this theory the gene complex for maleness may be represented as *A* and that for femaleness as *B;* another gene or complex, which may be indicated as *Z*, determines the sequence of activation or expression of *A* and *B*. *A* and *B* in themselves are believed to be relatively stable, but *Z*, which represents

TWELVE ***years ago, powdery mildew suddenly appeared in destructive form on melons in the Imperial Valley, Calif., the leading muskmelon-producing section in the United States. It could not be controlled by fungicides, and plant breeders began a search for disease-resistant material. In 3 years of careful testing they discovered several resistant varieties among melons imported from India. They were poor melons, but by suitable crosses their resistance to mildew was bred into good American varieties, and in another 4 years the first of the hybrids was released to California growers. Four more years of selection gave Powdery Mildew Resistant Cantaloup No. 45, which has superior shipping qualities in addition to disease resistance. This was released to growers in 1936, and the mildew problem is now largely solved in this area.***

the factors controlling the expression of maleness and femaleness, may be responsible for a reaction to environment that results in stimulation or retardation of *A* or *B* within very wide limits.

The pollination technique developed by Porter (*18*), working with watermelons, illustrates the general method employed in making controlled pollinations with flowers of the cucurbits. Approximately 24 hours before the flowers open, pistillate and staminate flowers are selected and covered with small muslin bags (in the case of melons and cucumbers, 1-pound manila bags are satisfactory). As soon as possible after the flowers open, the staminate flower is removed and its pollen is applied to the stigma of the pistillate flower. After pollination, the pistillate flower is covered with a 1-pound manila bag, held firmly in place by string or a paper clip. The pollination data are written on a tag attached to the flower, or directly on the paper bag. Several days after pollination the bags are removed, the fruit is tagged, and its location is marked by a stake.

It has been found unnecessary to cover the staminate flowers with a bag before they open. By placing a string around the corolla the flower is prevented from opening, and insects cannot enter. This eliminates one step in the process and increases the number of flowers that can be pollinated in a given length of time. Hermaphrodite flowers that are to serve as the female parent in a cross must not only be bagged before they reach full bloom but emasculated before the anthers shed pollen, to prevent self-pollination. Since the anthers may discharge pollen 24 hours before the flowers open, emasculation should be done more than 24 hours before opening. Purely pistillate flowers that require no emasculation need not be bagged before pollination, but the corollas may be tied shut as described above.

CUCUMBERS

THE cucumber, *Cucumis sativus* L., is supposedly a native of India (*30*), although plant explorers have never been able to discover a wild prototype. Cucumbers have been cultivated since earliest antiquity. Reliable records indicate that they were used as food in ancient Egypt, and were a popular vegetable with the Greeks and Romans. They are very important staple vegetables among the Russians and many orientals. In the United States cucumbers are widely grown in home gardens, in local-market gardens, and on truck farms for shipping, but in spite of their wide distribution under cultivation, their commercial importance is not so great as that of some of the other cucurbit crops.

Varietal Improvement

Cucumbers are usually divided into two classes according to use—slicing varieties and pickling varieties. This distinction is maintained even though the slicing variety may be used for both purposes. The plants of slicing varieties produce a moderate number of medium-length thick fruits generally with white spines. The pickling varieties are characterized by the production of very numerous, small, black-spined fruits. The fruits of most pickling varieties are so small, while still immature, that they are not adapted to slicing.

In England, a special forcing type of slicing cucumber is grown in greenhouses. This type sets fruit without any pollination and the fruits attain great length—over 2 feet in some varieties. Unless pollination is insured, the fruits are seedless, straight, dark green, and generally spineless. American consumers, however, do not like the huge English type, and American greenhouse varieties are either of the White Spine slicing type mentioned above or of an intermediate hybrid type somewhat longer than White Spine and darker green. Most growers of greenhouse cucumbers in this country use especially adapted strains; many use their own selections.

With one exception, all of our extensively grown commercial varieties of cucumber are the results of breeding, selection, or introduction by private growers and seedsmen. Many of the names commonly listed today are very old and represent varieties introduced from Europe. The origin of very few varieties is a matter of record, even in the case of comparatively recent introductions. Confusion in names is perhaps more extreme in cucumber varieties than in many other crops because of the ill-defined nature and lack of stability of so many of the supposed varietal characteristics. Vine habit, bearing habit, fruit size, shape, and color are all subject to marked variation under different conditions of culture, making the identification of varieties difficult. In all cucurbits, natural cross-pollination within a species complicates the problem of maintaining the purity and uniformity of stocks and varieties, but mixtures are especially difficult to detect in cucumbers because many so-called varieties have few really distinguishing features. With the exception of special greenhouse types and novelties, there are probably not over 15 to 20 really distinct cucumber varieties grown in this country.

It is questionable whether many of the supposedly superior varieties introduced successively in the last 50 years represented improvements distinct enough to justify new variety names. Seedsmen and growers have long attempted to develop varieties that will produce fruits of good size, uniform cylindrical shape, and attractive dark-green color before they begin to show signs of full maturity. Color is especially important because paleness or a yellowish tinge suggests too advanced maturity. A uniform dark green is most desired, and of course the flesh must be tender, crisp, and free from objectionable flavor.

A more recent breeding objective, not yet realized, is to develop varieties with a wide range of adaptability and resistance to various adverse conditions that result in low yields and poorly shaped fruits.

Early Cluster, Early Frame, Early Russian, Long Green, and White Spine were listed by the earliest seed catalogs in the United States, and have been grown here for at least 125 years. The first three are small, early, prolific varieties typical of the black-spined type; the last two bear larger, less numerous white-spined fruits that are more like the present popular slicing varieties. The origin of none of them is known.

Improved Long Green is a very long (12 to 13 inches), black-spined, dark-green, slightly tapered, late variety selected from London Long Green by D. M. Ferry & Co. and introduced in 1872. Arlington White Spine, a selection from White Spine that appeared about 1880,

is still a leading strain of White Spine. It is about 8 to 9 inches long, 2½ inches in diameter, medium green, and has a tendency to turn pale green or white at the blossom end. Davis Perfect (1905) was originated by Eugene Davis, of Grand Rapids, Mich., from a cross between White Spine and Telegraph, an English forcing variety. Davis Perfect is about 10 inches long, 2½ inches in diameter, white-spined, smooth, dark green, and distinctly tapered at both ends. Fordhook Famous, introduced by W. Atlee Burpee & Co. in 1902, was originated by A. McInnis, a grower in Ontario, Canada, who selected it from a cross of White Spine and Noa Forcing, made about 1894. It is a typical White Spine type, showing but little of the Noa Forcing character. Early Fortune was selected from a field of Davis Perfect by George E. Starr in 1906 and introduced by the Jerome B. Rice Seed Co. This has been an important and popular White Spine type for many years on account of its desirable size (about 8½ by 2½ inches), attractive cylindrical shape with rounded ends, good retention of green color, and productivity. Other popular current varieties are Stays Green or Black Diamond, Klondike, and Longfellow. The origin of these is obscure.

Deltus, a popular forcing variety, was obtained from a cross between White Spine and Tailby Hybrid made in 1896, the progeny of which was later crossed with Long Green. Adelbert Titus, a grower near Rochester, N. Y., originated the variety. Another popular variety of the Rochester district is the Irondequoit, developed by J. H. Wirt & Sons from a cross of White Spine and Telegraph made in 1904. In 1929 the New York Agricultural Experiment Station at Geneva, N. Y., introduced a parthenocarpic (seedless) variety named Geneva. It was developed from a cross of Arlington White Spine × Rochford Market made in 1916. All three of these are intermediate between the White Spine and the English types.

It is evident that the old White Spine is involved in the parentage of nearly all the slicing varieties grown in this country, both field and greenhouse types. Except in cases of known hybridization with Black Spine or English forcing sorts, one might be justified in considering all our white-spined field types simply as strains of White Spine.

Of the pickling type, Boston Pickling (1865), Chicago Pickling (about 1880), National Pickling (1929), and Snow Pickling (1906) are by far the most important. The first two are selections from unknown varieties grown near the places of origin indicated by the names. Snow Pickling was introduced by J. C. Snow, of Rockford, Ill., in 1906. National Pickling was developed by George E. Starr, of the Michigan Agricultural Experiment Station (1929), to meet the specifications of the National Pickle Packers' Association, who cooperated with the station in the work. The pickle packers desired a variety producing a large number of small, black-spined, dark-green fruits, similar to Snow Pickling but more nearly cylindrical or blocky, having the same diameter well out to the ends instead of being slightly tapered. These specifications are of special interest to those who pack pickles in glass containers and desire the most attractive product possible.

Disease Resistance

Reference to the appendix at the end of the section on vegetables in this Yearbook will show that several investigators, both in the United States and abroad, are trying to develop good commercial varieties having resistance to one or more of several diseases, particularly mosaic, downy mildew, and bacterial wilt.

Mosaic is a serious problem wherever cucumbers are grown in the Central, Eastern, or Southern States, particularly in the areas devoted to pickling varieties. Losses of 15 to 30 percent of normal production may be expected annually, and in many isolated cases much heavier losses occur.

Downy mildew is generally distributed. It is especially severe in the South, where it is in effect the dominant limiting factor in cucumber production. The losses usually depend on how early the disease attacks the plants, for it occurs every year and terminates harvesting soon after it becomes established in a field. Thorough spraying two to three times weekly is often an inadequate although a very expensive attempt at control.

Bacterial wilt is a serious disease, in the Central and Eastern States in particular. Plant pathologists estimate general losses to be 10 to 20 percent of a normal crop, while often certain fields may be practically a total loss.

The Bureau of Plant Industry has obtained a number of stocks of oriental varieties of cucumbers, chiefly from China, Japan, and India, some of which contain distinctly disease-resistant individuals. Considerable tolerance to mosaic has been found in certain inbred lines, and in some a measure of resistance to mildew and to wilt. High-quality American susceptible varieties have been crossed with the low-quality resistant kinds and the hybrids back-crossed to the American parents. Inbreeding is also being continued in efforts to isolate lines that are pure (homozygous) for resistance to specific diseases.

Bailey and Burgess, at the Maine Agricultural Experiment Station, are engaged in breeding cucumbers resistant to scab. This disease causes very severe losses by spotting the fruits, making them unsalable, as well as by reducing yields. It is confined almost entirely to the northernmost States. Inbred lines of commercial varieties are subjected to artificial inoculation to determine resistance or susceptibility. A number of lines apparently homozygous for resistance have been isolated. Preliminary studies indicate that resistance is dominant and due to a small number of factors, possibly only one.

MUSKMELONS

It is generally believed that the muskmelon (*Cucumis melo* L.) is native to India (*30*). Although there are indications that it was in use about the beginning of the Christian Era, it is not believed to have been in cultivation in very ancient times.

From its center of origin in northwest India it spread to China and Japan but has not reached a high state of development in those lands. To the westward, in Iran (Persia), in Turkistan, and in other regions of Asia Minor and about the Mediterranean, it was developed to a very

high state of perfection. Columbus first brought the species to the New World, and the natives of the West Indies and the mainland of North America quickly adopted it. By 1535 it was grown by the Indians as far north as Montreal, Canada.

Although the muskmelon is grown in every State, most of the commercial production is concentrated in a few sections of southern California, Arizona, Colorado, Texas, Michigan, and Indiana and in the tri-State area of Maryland, Delaware, and New Jersey.

There is a large number of varieties of muskmelons under cultivation in the United States. Many of them closely resemble one another, and improved forms are gradually replacing the older varieties. Muskmelon varieties may be arbitrarily divided into two classes—(1) shipping or commercial melons and (2) local-market and home-garden melons. Most shipping varieties produce comparatively small fruits with a tough rind and firm flesh and are adapted for shipping in standardized packages to distant markets. Local-market melons generally have softer flesh and are often large.

The name "cantaloup" is quite generally used in the United States to designate the small, oval, netted shipping type of muskmelon. Much confusion over the term has resulted from the fact that in Europe it is applied to a different type of melon, a long-keeping sort with a hard, ridged or warty rind, practically unknown to American growers (*14*). The American usage is now so well established that we must accept the name cantaloup as defined above. Obviously all cantaloups are muskmelons, but many varieties and types of muskmelons are not cantaloups by this definition. The kinds that lie outside the definition are the winter types, as Persian, Casaba, and Honey Dew, the Honey Ball, and the large, ribbed sorts like Bender and Montreal.

Varietal Improvement and Breeding

The number of varieties of muskmelon that have been and are being grown in this country is so great that no attempt to review the early history and development of all of them can be made here. Only the leading present varieties and a few of their supposed progenitors can be discussed, together with a brief reference to certain kinds that were formerly important.

Prior to 1850 most of the few varieties of muskmelon then grown in this country were introduced from Europe. Efforts were begun prior to that time to improve the crop from the standpoint of adaptability, particularly to the northern part of the country. Increased earliness and productivity were of special interest, since most of the imported varieties then available were apparently from warmer regions or for greenhouse culture. Nutmeg and Pineapple appear to have been varieties similar to our present cantaloups, and apparently the famous Netted Gem—later called Rocky Ford—was derived from the latter. Pineapple was described by Burr (1865) as roundish to oval, without ribs or with ribs faint, size small, skin olive green with abundant net markings. Nutmeg was described as slightly larger, ribbed, and otherwise similar. Both were old well-known European types. Most sorts described at that time were large, heavily ribbed, and netted. Numerous melons of the winter Casaba

or Persian type were described, but there is no indication that they were important. Most of the supposed American varieties mentioned by Vilmorin in 1856 were indicated as being related to the "American" variety Pineapple.

One of the earliest instances of muskmelon improvement in this country was the origination of the Christiana melon. It was developed about 1835 by Josiah Lovett, of Beverly, Mass., and is supposed to have been a cross of the variety Green Malta and an unnamed early sort. Despite poor quality, it was popular because of its earliness and was commonly listed for over 75 years.

About 1875 keen interest in muskmelon improvement was shown by both seedsmen and growers for the market, but the latter were perhaps the more active in actual selection and hybridization. Little artificial pollination appears to have been done, but natural crossing in mixed plantings furnished these growers with an abundance of material for selection.

About 25 rather distinct varieties besides the winter melons are of commercial importance or considerable home-garden interest and are listed by the leading seedsmen of this country at present. About a third of these are over 50 years old and only a half dozen are less than 25 years old. This survival indicates that the old "practical breeders" achieved results not easy to surpass and that the introducers brought in varieties well adapted to cultural conditions and consumer tastes. In 1901 there were about 25 or 30 fairly distinct and important sorts commonly listed, and about half of these are still current.

The old Surprise, of unknown origin, was introduced in 1876 and is supposedly the parent of Bender Surprise, a large, prominently ribbed sort that is an important home and market melon of the Northern States today.

The Netted Gem, apparently a form of the very old Pineapple, was first listed by W. Atlee Burpee & Co. in 1881. Its notably successful adaptation to shipping and market needs stimulated a great deal of interest in obtaining different and still better varieties of the same general type. Varieties of this type, with different flesh colors, slightly different sizes and shapes, and adaptability to different regions, soon were developed in the commercial muskmelon areas.

In 1886, Acme or Baltimore was introduced by J. Bolgiano, of Baltimore, and Emerald Gem, by W. Atlee Burpee & Co. Anne Arundel, introduced by Griffith & Turner, of Baltimore, in 1894, was believed to have been selected from Acme. About 1905 another selection, apparently from the Acme-Anne Arundel line of development, was introduced under the name of Sweet Air by George Tait & Sons, of Norfolk, Va. This same variety had been sold in Maryland as Knight for some years. The two names are known to be synonymous and the variety is still widely grown in the Chesapeake Bay section.

In 1897 the Netted Gem was renamed Rocky Ford to advertise its merits as grown and shipped by a group in the Rocky Ford, Colo., district, whereupon it became more popular than ever. When it proved to be adapted to the Imperial Valley, that desert area having been placed under irrigation a few years later, a truly phenomenal development of the cantaloup industry began. Several years later, green-

fleshed selections with salmon-tinted cavity were made from Netted Gem or Rocky Ford and appeared as Salmon Tint and Pollock 10–25; and deeply salmon or orange-fleshed selections appeared as Perfecto (1919) and Superfecto (D. V. Burrell & Co., 1926). These improved varieties of the Netted Gem type are more nearly spherical, more heavily netted, and thicker fleshed than the parent variety, and the present vogue is for solid salmon-colored flesh. They also differ somewhat in adaptation to climate, culture, and handling methods.

Hale Best, introduced in 1924 by I. D. Hale, became the leading commercial or shipping variety. It was developed by selection from a mixed stock obtained from a Japanese gardener in the Imperial Valley. The vines are medium in size; fruits small, usually weighing 2 or 3 pounds each, oval to round, slightly ribbed, well covered with dense heavy netting; flesh thick, firm-textured, solid salmon in color. Hale Best is the earliest of the high-quality shipping melons. The variety was quite variable when introduced, but improved forms have been and are being developed. Hale Best No. 36 and Hale Best No. 112 are popular strains at present. Since the variety is susceptible to mildew, it is certain to be displaced, at least in the Imperial Valley, by the new mildew-resistant varieties.

Hale Best is similar to Perfecto but is usually a few days earlier. The fruit is somewhat larger and the flesh possibly firmer, and it tends to hold up in shipment longer than Perfecto. Superfecto and Perfected Perfecto (Garwood & Woodside, 1925) are improved strains of Perfecto.

It is rather striking to note how the old Acme type and its elongate, green-fleshed descendants have tended to dominate the field in the Middle Atlantic States while the Netted Gem and its nearly round, salmon-fleshed derivatives have moved West and dominated that area from the beginning of the industry. Two other types or lines of development, from Osage, are also of particular interest, since the varieties that have resulted from them compete more or less with the two types just mentioned.

The Osage was originated by Roland Morrill, an active muskmelon breeder of Benton Harbor, Mich. It is claimed that it was selected from a natural cross of Orange Christiana and "a small black melon obtained from a Swedish gardener on the Osage River in Missouri", about 1880. It was introduced by Vaughn's Seed Store in 1887. Some believe that Osage is a selection from Miller Cream, with which it is now synonymous, regardless of its possible origin. Miller Cream was developed by J. D. Miller, of Elmira, N. Y., from a supposed cross of Sills Hybrid and Casaba. About 1890 one of Morrill's associates discovered a single plant in a field of Osage that was believed to be a cross between Osage and Netted Gem. Selection from this plant ultimately produced the variety Hearts of Gold that was introduced about 1895 or 1900. Morrill is said to have sent seed of certain selections from this supposed Osage × Gem cross to Paul Rose for trial, and the latter selected and introduced the varieties Paul Rose (also called Petosky and Osage Gem) about 1898 and Hoodo about 1900. Both were very similar to Hearts of Gold. Hoodoo and Hearts of Gold now are considered synonymous. It is further reported that from Osage Gem D. M. Ferry & Co. selected a strain named

Defender, introducing it in 1901; and that Burrell Gem is a strain of Defender, introduced by the D. V. Burrell Seed Co. in 1904. Burrell Gem and Defender are now synonymous. In 1907 D. M. Ferry & Co. introduced Extra Early Osage, a distinctly earlier variety of the Osage type.

Most varieties that attained importance and later practically disappeared are of unknown origin, although a few are of interest as examples of early purposeful hybridization. Cosmopolitan, introduced in 1894, was from a cross between Green-fleshed Malta and an unnamed netted type. Christiana has been mentioned.

The probable interrelations of some of the important muskmelon varieties are given in figure 2.

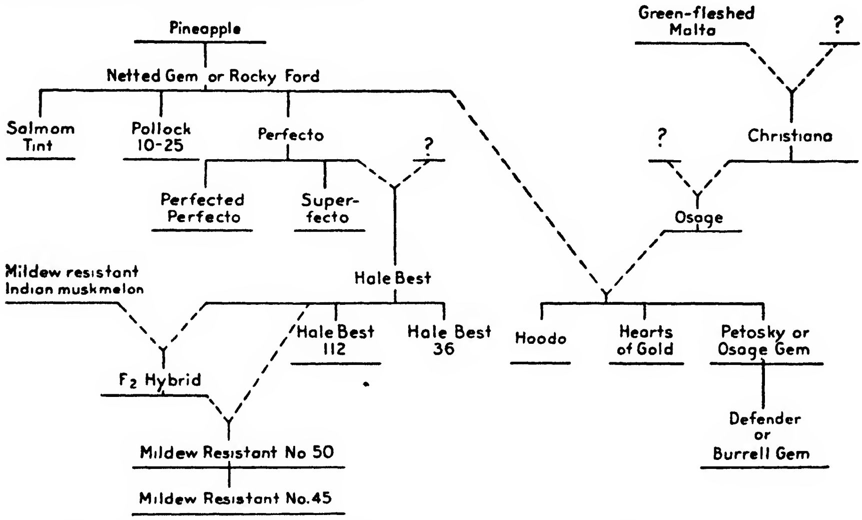

Figure 2.—Probable interrelations of some important muskmelon varieties.

Some old varieties still commonly listed are of unknown origin, but the date of introduction is known. These include Banana (1884), Texas Cannon Ball (1894), Hackensack (1883), Jenny Lind (1866), Montreal (1884), Tip Top (Livingston Seed Co., 1892), Eden Gem (1905).

Among more recent results of introduction and breeding should be mentioned Fordhook (Emerald Gem × Jenny Lind), introduced by W. Atlee Burpee & Co. in 1908. Honey Dew (the old French variety White Antibes Winter) was introduced into the United States about 1900. It not only became popular, but has also often been used as a parent in attempts to introduce its particular quality and flavor into varieties of the cantaloup type. Honey Ball is an important hybrid of Honey Dew and Texas Cannon Ball developed by W. H. Parker, a Texas grower. The original cross was made in 1916 and the variety introduced in 1924 by the Robert Nicholson Seed Co., of Dallas, Tex. Honey Rock is said to have been produced by crossing Champlain, Irondequoit, and Honey Dew. It was introduced about 1920 by Watt Richardson, of Ohio.

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The origins of the Persian and the winter (Honey Dew and Casaba) types of melon are unknown. They are very old varieties and were introduced from Europe and Asia.

The Japanese melon is a distinct new variety that has become popular in the local markets of California. It is worthy of trial in other sections with a long growing season. The fruits are fairly large, round, flattened at the blossom end; the rind is tender, thin, pale grayish green with dark blotches, sparsely netted, and very slightly ribbed. The flesh is light salmon in color, soft, and juicy.

In the new variety, Weaver Special, the white rind of the Honey Ball is combined with the salmon flesh of the shipping-type cantaloup. It was selected from a cross by J. C. Fluke, of C. H. Weaver & Co., in the Imperial Valley, and introduced to the trade in 1933.

Figure 3.—J. T. Rosa (1895–1928), who made important contributions to the breeding of cucurbits, particularly muskmelons and watermelons.

Breeding for Disease Resistance

Thirty or more years ago growers noticed differential susceptibility of muskmelon to certain diseases. Hoodoo was mentioned as being resistant to blight.

In 1904 Blinn (*1*), of the Colorado Agricultural Experiment Station, started mass selection in the Rocky Ford variety in efforts to obtain strains resistant to rust (*Macrosporium cucumerinum* Ell. and Ev.). Beginning in 1906, progenies from individual plants and fruits were studied and subjected to selection under severe rust-infection conditions. Although selections were from open-pollinated individuals, marked success was obtained and strains of high commercial value were readily established. The andromonoecious habit of the variety resulted in less cross-pollination and mixture of strains than might be expected to occur in other varieties and species of curcurbits. Blinn also selected for superior shipping and eating quality and developed the first of the salmon tint strains of the Netted Gem type.

In 1925 powdery mildew (*Erysiphe cichoracearum* DC.) suddenly appeared in destructive form on melons in the Imperial Valley of California. Fungicides were found to be inadequate in controlling the trouble, and the crop was seriously injured for the next several seasons.

In searching for resistance, melon varieties and strains from all parts of the world were grown by J. T. Rosa (fig. 3), of the California Agricultural Experiment Station, and I. C. Jagger, of the United States Department of Agriculture, in the Imperial Valley in 1926, 1927, and 1928 (*12*). There was no appreciable success until 1928.

In that year numerous plants were found in several unfixed varieties from India that were practically free from mildew throughout the season, while other plants of the same varieties, and all plants of many other varieties, were badly injured. Unfortunately, the fruits of all the mildew-free plants were commercially useless because of poor shipping and eating qualities. Several commercial varieties were immediately crossed with the mildew-free plants. Resistance to mildew appeared to be inherited as a simple dominant Mendelian character. Back-crossing has considerably hastened the production of varieties that combine the resistance of the Indian melons with

Figure 4.—Comparative test of mildew-resistant and susceptible varieties of muskmelon in the Imperial Valley, Calif.: *A*, Powdery Mildew Resistant Cantaloup No. 45 is practically mildew-free; *B*, Hale Best has leaves largely destroyed by the disease.

the shipping and eating qualities of the American varieties. The development of resistant strains has now largely solved the mildew problem in this area.

Powdery Mildew Resistant Cantaloup No. 50, distributed for commercial trial in 1932, was the first fully resistant variety developed. The fruits are quite variable in size, shape, and quality. It was produced from a cross between the Hale Best variety and one of the resistant plants in the Indian varieties. Individuals from the F_2, or second hybrid generation, were backcrossed to Hale Best, and this was followed by two additional generations of selection. Starting with No. 50, four more generations of selection finally gave Powdery Mildew Resistant Cantaloup No. 45 (fig. 4), grown commercially for the first time in 1936. No. 45 is quite uniform in size, shape, and quality (fig. 5). It resembles Hale Best, but matures somewhat later. The flesh

has even a firmer texture than that of Hale Best. This characteristic gives promise of making it a superior shipping melon in districts adapted to its production

Powdery mildew-resistant strains of Honey Dew and Honey Ball are being developed for the Imperial Valley under the same project and

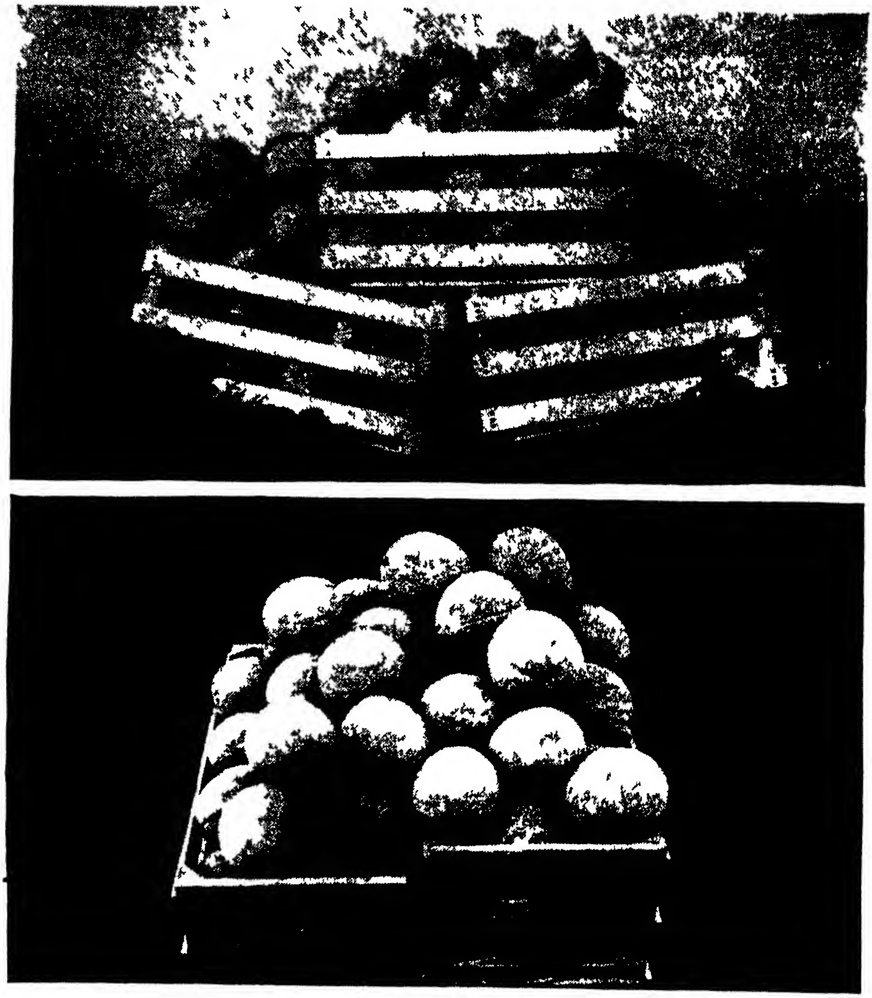

Figure 5.—Powdery Mildew Resistant Cantaloup No 45, showing type and uniformity of field run melons.

by similar means Powdery Mildew Resistant Honey Dew No 60 has been in commercial use in this district since 1935. Outside of freedom from mildew, it has not been quite so satisfactory from a commercial viewpoint as the standard Honey Dew. Backcrossing with Honey Dew and further selection should correct its objectionable characters

WATERMELONS

The watermelon, *Citrullus vulgaris* Schrad., is supposed to have been in cultivation some thousands of years, because it had a name in ancient Sanskrit. It is believed to be native to tropical Africa. In 1857, David Livingstone reported it as growing profusely in the Kalahari Desert after an unusually heavy rainfall. Both edible sweet and inedible bitter forms were present. The natives prized the sweet ones highly and made long journeys to obtain them. In parts of Africa the watermelon is a very important crop, furnishing not only food but also drink during periods of drought. In parts of the Union of Soviet Socialist Republics the fruits are important as a staple commodity, being pickled, used as a source of sirup, and eaten fresh. In parts of China certain firm-fleshed varieties are cut into strips, dried, and then made into pickles, sirup, preserves, or glacé sweets. The commercial production and shipping of watermelons to distant markets, to be used fresh, is much more extensive in the United States than anywhere else in the world. Although the crop is grown for home use and local markets in nearly every State, its culture for shipping is confined to the Southern States and to California.

In this discussion the word "type" is occasionally used in referring to groups of varieties of watermelons. It is admitted that the term is loosely used, for there is no single basis for classifying American watermelon varieties that is generally accepted as being adequate. They might be classified according to general features of shape and color, but that would bear no relation to use or to other qualities. A classification according to use, whether for home and local use or for shipping, would denote something concerning eating quality and rind characters, since the favorite varieties of any crop for home and local use are those that are highest in eating quality but are often too perishable for long-distance shipment. Within these two large classes, however, would be found nearly the whole range of colors and shapes. Any attempt to identify a few distinct types, all of which possess numerous qualities in common, presents perplexing difficulties. The problem is to establish a basis of classification in which the individual types are neither too exclusive nor too inclusive to be of practical value.

Varietal Improvement

A hundred years ago varieties of watermelon were ill-defined and seedsmen's listings usually referred to types rather than to varieties in the modern sense. With the exception of Bradford, which is still listed by a few dealers, no variety mentioned previous to 1850 is listed today, but a few were still common in the early 1900's. Among these were Black Spanish, imported from Portugal in 1827; Carolina, known in 1825; Imperial, Mountain Sprout, Seminole, and Mountain Sweet, introduced by southern growers around 1840 to 1850, or before. Bradford, Clarendon, Odell, Ravenscroft, and Souter all originated in South Carolina sometime prior to 1850.

Although the leading shipping varieties of today are comparatively recent developments, three home and local-market melons still listed by dealers are 60 to 75 years old. Peerless or Ice Cream was introduced in 1860, Phinney Early in 1870, and Georgia Rattlesnake about 1870 by M. W. Johnson, of Atlanta, Ga.

As in many other vegetable crops, the period from 1880 to 1900 marked the beginning of active varietal development and introduction by growers. A large proportion of the varieties listed at present were introduced during that time, and many of them are unsurpassed by later developments except in carrying better quality and disease resistance. The originators or introducers of only a few are now known, and the parentage of even fewer.

W. Atlee Burpee & Co. introduced Cuban Queen in 1881. Round Light Icing appeared in 1885. Kolb Gem, originated by Reuben F. Kolb, of Alabama, was introduced in 1885 by D. M. Ferry & Co. Hungarian Honey apparently was introduced from Hungary about 1885 by persons now unknown. Florida Favorite, said to be a cross between Pierson and Georgia Rattlesnake, was introduced by Girardeau, of Monticello, Fla., in 1887. Dark Icing was brought out by D. M. Ferry & Co. in 1888. Gray Monarch or Long Light Icing appeared in 1889.

Dixie was produced by George Collins, a North Carolina grower, and introduced by Johnson & Stokes in 1890. Stories differ as to whether Cuban Queen or the old Mountain Sweet was one of the parents, but they agree that Kolb Gem was the other. Cole Early was introduced by Cole's Seed Store, Pella, Iowa, in 1892. Sweetheart was developed by a Mr. Wittenmeyer of southern Indiana about 1890 and introduced by D. M. Ferry & Co. in 1894. One of the superior varieties, in eating quality, is Kleckley Sweet, developed by W. A. Kleckley, an Alabama watermelon grower. Its popularity and quality encouraged renaming, and Monte Cristo is one synonym that has persisted. It is said to be from a cross of Boss and Arkansas Traveler (introduced 1892). W. Atlee Burpee & Co. introduced the variety in 1897.

The Chilean, a variety, or perhaps more accurately a type, introduced from the west coast of South America, was first grown in California about 1900. Both white-seeded and black-seeded strains of this variety are now available and are extensively grown in the West. Angeleno was introduced to the trade by Johnson & Musser, of Los Angeles, in 1908, although it had been grown locally for some time. Its origin is obscure, but it is believed to have been selected from a South American stock related to Chilean. White-seeded and black-seeded strains are available, and they possess unusually dark red interior color and high quality. Another variety that gained prominence in the West is Klondike. Its origin is unknown, but it appeared about 1900. Solid-green and striped strains are grown. These three varieties are dominant in California at present and are hardly known elsewhere. Conversely, the important varieties elsewhere are largely unknown in the Pacific coast and southwest areas.

D. H. Gilbert, of Monticello, Fla., introduced Excel in 1906. The origin of Excel is not clear, but it was evidently a poorly fixed intervarietal hybrid. The introducer has stated that the original stock persisted in showing off-shape melons and variations in seed color. A white-seeded strain, introduced in 1926, was said to be free from these objections.

Tom Watson, the dominant shipping melon for the last 20 years or more, originated in Georgia and was introduced in 1906 by the

Alexander Seed Co., Augusta, Ga. It is a large, long, dark-green melon, with a thick, tough rind, that ships well. Unfortunately, however, the quality is only medium.

The original Irish Gray is reported to have been a volunteer plant found growing in an unoccupied stock-feeding pen by Charles Renew, of Rebecca, Ga., in 1913. Some believe the chance seed from which the variety was increased was brought in with feed imported from South America, but there is no proof of such an origin. In 1917 it was being shipped in carload lots, and it was doubtless second in importance in the early 1920's. It has yielded place, however, to Thurmond Gray, a variety originated and introduced by a Mr. Thurmond, a watermelon grower of Perry, Ga. Thurmond Gray first became prominent in 1923.

Stone Mountain originated in Georgia, near Stone Mountain, and was introduced in 1924 by the H. G. Hastings Co., of Atlanta. This melon is round or nearly so, green, of good quality, and a fair shipper. The vines are said to be prolific and resistant to foliage diseases.

The California Agricultural Experiment Station has effected some substantial improvements in uniformity, flesh color, eating quality, and shape of several varieties through the careful selection of lines inbred for several generations. California Klondike (from Klondike) was introduced in 1933, striped Klondike (from stock of the same name) in 1936, and Long Mountain (from Stone Mountain) in 1936.

In 1932 the Minnesota station introduced an unusually early variety, Northern Sweet, that extended the culture of the watermelon farther north. It was developed by inbreeding and selection from a stock introduced from the Union of Soviet Socialist Republics.

The Oscar H. Will Seed Co., of Bismarck, N. Dak., has introduced two varieties designed for growing in the northern Great Plains—Will Sugar in 1889 and Golden Anniversary in 1934. The latter is from a cross of Wikara × Kleckley Sweet, and the other from an unrecorded cross.

Breeding for Wilt Resistance

Until comparatively recently watermelons have been given very little attention by scientific workers. The work of Orton (*17*) is of more than ordinary historical interest, since it is one of the first recorded attempts of a plant breeder to synthesize a commercial variety resistant to a particular disease. Orton crossed the nonedible wilt-resistant citron melon with the edible wilt-susceptible watermelon variety Eden. From a large second-generation hybrid population, selections were made of plants with potentially desirable characters. By further selection a wilt-resistant edible variety, Conqueror, was produced in 1911. This variety never became a popular commercial type on account of unsatisfactory market and eating qualities.

Fusarium wilt is perhaps the most serious watermelon disease today, preventing profitable culture of susceptible varieties in many localities.

Wilt-resistant strains of commercial importance have been developed by Porter and Melhus (*19*) at the Iowa station, by selection from crosses of Orton's wilt-resistant variety Conqueror and certain commercial varieties. The two varieties developed by crossing (Iowa Belle and Iowa King) were about 65 percent resistant compared to the

1-percent-resistant commercial varieties. The exact origin of these two varieties is rather uncertain, but they were selected from apparently chance hybrids between Conqueror and one of the commercial varieties. Porter and Melhus also developed Pride of Muscatine, about 50 percent resistant, by selection of an inbred line of Kleckley Sweet. These three varieties were introduced in 1930.

The Florida station released a new wilt-resistant watermelon in 1936, the Leesburg, developed by M. N. Walker by pure-line selection in Kleckley Sweet grown on heavily infested soil.

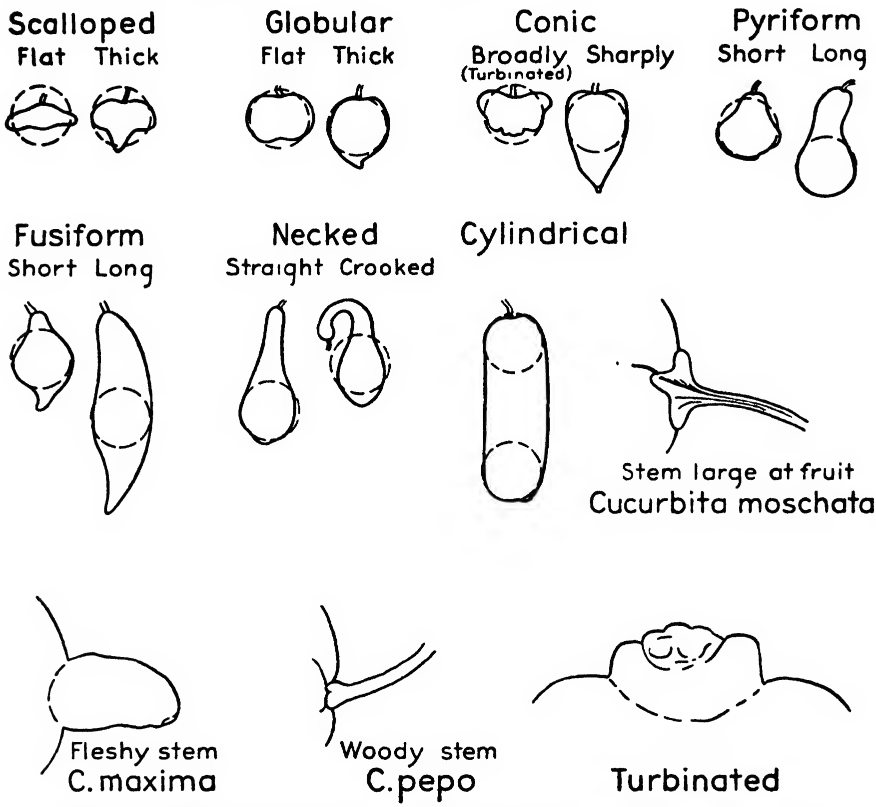

Figure 6.—Fruit shapes of varieties and stem characters of *Cucurbita* species.

The California station in 1936 introduced Resistant Klondike No. 7, a wilt-resistant sort selected from a cross of Iowa Belle × Klondike.

PUMPKINS AND SQUASHES

Pumpkins and squashes (*Cucurbita pepo* L., *C. moschata* Duchesne, and *C. maxima* Duchesne) are undoubtedly of American origin. Erwin (*6*) states that he has been able to identify fragments of stems, seeds, and fruits of *C. pepo* and *C. moschata* recovered from the cliff dweller ruins of the southwestern United States. With the help of archeologists, Erwin has determined that some of the material is from the basket makers, whose civilization antedates that of the

cliff dwellers; indeed, they were probably the oldest agricultural people of whom we have any record on the North American continent. Vavilov (*30*) believes that *C. moschata* originated in the Mexican-Central American region and that *C. maxima* originated in the Peruvian-Colombian-Ecuadorean area.

Pumpkin and squash varieties are numerous, but many are of local importance only. The fruits of the summer squash are used in an immature stage, while the rind is still tender. There are three important types—scallop, crookneck, and marrow or Italian. Each is represented by a number of varieties. Winter squashes and pumpkins are used when fully mature, after the rind has hardened. Hubbard is the leading type of winter squash, and Connecticut Field and Small Sugar are the leading pumpkins.

As has been previously stated, the differentiation of pumpkins from squashes is very uncertain, because as popularly classified there are both pumpkins and squashes in all three cultivated species of *Cucurbita*. Castetter and Erwin (*2*) have proposed that all varieties belonging to *C. pepo* and *C. moschata* be classified as pumpkins and the varieties of *C. maxima* as squash. Adoption of this classification would mean including the summer squash with the pumpkins, and various other changes in present popular usage. To seed growers and plant breeders the species are important, since varieties of the same species cross very readily, while those belonging to different species practically never cross in nature, contrary to popular belief. Figure 6 illustrates some of the principal differences among these three species of *Cucurbita*, and figure 7 illustrates stem characteristics.

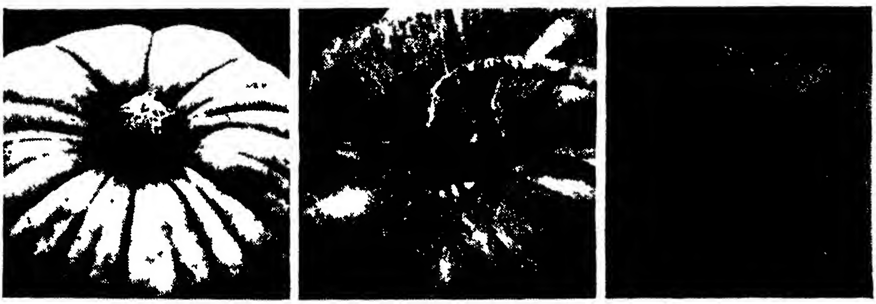

Figure 7.—Stem characters typical of the three species of pumpkin and squash. *A*, *Cucurbita pepo*; note five-angled stem not expanded next to fruit. *B*, *Cucurbita moschata*; stem neither angled nor fleshy but much expanded at attachment to fruit. *C*, *Cucurbita maxima*; stem neither angled nor expanded but fleshy and enlarged, becoming rather spongy when mature.

Varietal Improvement

A study of the origin of our present varieties of pumpkin and squash would require delving into colonial history, and in a number of cases the trail of a variety appears to lead into the history of Indian tribes, where it can no longer be followed.

Large Cheese and Connecticut Field pumpkins were common under those names before the Revolutionary War. Small Sugar is doubtless a hundred years old. The Cushaw has been listed in catalogs for

nearly a hundred years and represents a distinct form, perhaps a variety, that was being grown by the Indians in 1586.

Of the winter squashes, Acorn, a Turban form, was listed over a hundred years ago. Boston Marrow was described by Burr in 1865 as synonymous with Autumnal Marrow. This variety has been widely grown under one of these names in the United States and Europe for a hundred years. John M. Ives, of Salem, Mass., discovered its merits in 1831 and popularized it. He obtained the seed from a friend in Buffalo, N. Y., who in turn is said to have obtained it from a tribe of Indians (unnamed) that visited Buffalo periodically. The Hubbard was introduced to the trade by J. J. H. Gregory, a seedsman of Marblehead, Mass., about 1855. He stated that it had been introduced in the vicinity of Marblehead some 60 years before. The variety is thus conservatively 150 years old and probably older. Marblehead, also introduced by Gregory, is thought to have been imported direct from the West Indies about 1865. Winter Crookneck was described accurately, though not under that name, in 1686 and has been listed in seed catalogs for about a century.

The summer squash varieties are also very old. Both White Bush Scallop and Yellow Bush Scallop were common in 1865, and Burr says the yellow variety had been common for over a hundred years at that time. They were being shipped from the South to northern markets before the Civil War. Yellow Summer Crookneck and various forms of Vegetable Marrow [2] like some grown today have been listed in catalogs for over a century and are believed to have been in common use much longer than that. Three additional varieties—Italian Vegetable Marrow (before 1850), Cocozelle (Vilmorin, 1856), and Mammoth (1826)—were listed by seedsmen and described at the dates indicated; but some or all of them are certainly older, if we may judge by their importance and widespread distribution as stated or implied in the early references. A few variety names of 75 to 100 years ago have almost entirely disappeared from our catalogs and modern literature, but very few, among them Sweet Potato, common about 1850; Valparaiso (1827); and Yokohama, introduced from Japan about 1850.

Is there anything new in squash or pumpkin? Few distinct varieties have been introduced in the last 50 years that are superior, or even equal, to the important old-timers mentioned. Pikes Peak, a winter squash said to have originated in Iowa, was introduced in 1888. Fordhook was introduced by W. Atlee Burpee & Co. in 1889. Des Moines or Table Queen is said to have been introduced from his native country by a Danish farmer about 1900. It was 15 to 20 years later that it became popular and acquired its present name. Delicious, probably a selection from Hubbard, was introduced by Gregory in 1905. Golden Hubbard was introduced in 1896 by a Mr. Harrison of Painesville, Ohio. It was found as a chance plant in a field of Hubbard.

Because of their adaptability to pollination by insects, pumpkin and squash varieties and stocks are difficult to maintain free from mixture. This characteristic also is a prolific source of variation even within

[2] Vegetable Marrow designates a group of summer varieties of *C. pepo* or summer squash characterized by oval or elongate, cylindrical fruits that are harvested for use in a quite immature stage. Cocozelle and Zucchini are common varieties of Vegetable Marrow.

good stocks. In recent years numerous seedsmen have taken greater care in isolating selections made with specific objects in view. As a result, there are now available many good strains that represent improvements in uniformity, earliness, quality, and appearance overthe old parent stocks. The State experiment stations have proved the value of inbreeding in isolating superior, highly uniform strains, and their work indicates the practicability of selecting, from this g roup that has such rich potentialities, strains that will meet almost any set of specifications desired.

Twenty-five years ago Cummings and Stone (*4*), at the Vermont station, initiated their important studies of selection in open-pollinated and inbred lines of Hubbard squash with reference to yield, chemical composition, and quality. The Vermont Hubbard, an inbred line, was introduced in 1914, along with other slightly different strains. Some 6 years later the Vermont workers introduced Long Storage Hubbard, an inbred strain selected specifically for superior storage qualities. About 1921 Bushnell and others of the Minnesota station introduced Kitchenette, an earlier, smaller type of Hubbard produced by inbreeding and selection. In 1932 Krantz and others at Minnesota introduced a very large inbred selection from Hubbard under the name of New Brighton.

In 1932 Yeager and Latzke (*34*), of the North Dakota station, published an account of the development of their new Buttercup squash. This variety is of particular interest because it resulted from a breeding program designed to develop a highly productive, high-quality, highly nutritious squash, adapted to northern Great Plains conditions, as a substitute for the sweetpotato—meaning the real sweetpotato, not the Sweet Potato variety of squash. Inbred selections from a chance cross of Quality×Essex Hybrid best met these specifications. Buttercup is a small (3 to 3½ pounds), yellow, neat, Turban-like variety with flesh of an unusually high solids content (25 percent and higher), containing about 15 percent of starch, 5 percent of sugar, and 2.5 to 3.0 percent of protein. It came from a wide cross and has been difficult to make uniform.

Other varietal improvements have been made to meet specific market demands. In 1936 the California station introduced Gray Zucchini, an inbred strain of Zucchini, and the Connecticut station introduced Connecticut Straight Neck from a Straight Neck inbred× Golden Summer Crookneck.

INHERITANCE IN THE CUCURBITS[3]

CYTOLOGICALLY this family has proved to be less interesting than the vast amount of variation within the group would indicate. Furthermore, the material does not lend itself easily to cytological investigation by the ordinary methods. Although a long list of genera and species has been investigated, there are no established cases of polyploidy, fragmentation, or other gross chromosomal phenomena. Of the cucurbits, cucumbers (*Cucumis sativus*) have 7 pairs of chromosomes, muskmelons (*C. melo*) have 12 pairs, watermelons (*Citrullus vulgaris*) have 11 pairs, and the pumpkins and squashes (*Cucurbita pepo*, *C. moschata*, and *C. maxima*) have 20 pairs (*31*).

[3] This section is written primarily for students or others professionally interested in breeding or genetics.

Inheritance in Cucumber

Information regarding the hereditary behavior of specific characters in the cucumber is very meager. It has been shown that (1) spininess is dominant over spinelessness; (2) black spines are dominant over white ones; and (3) the tendency toward the production of fruit lacking viable seeds (parthenocarpic fruit) is apparently associated with black spines, suggesting that these factors are linked.

Some recent work by Hutchins (*10*) has uncovered an interesting green-flowered variation. This variant is female sterile. As a result, the characteristic can be carried along only in the heterozygous condition. Tests with the normal yellow-flowered form indicate that this green-flowered character is dependent on a single gene recessive to normal yellow, the second-generation hybrid population segregating into 3 normal yellow plants to 1 green-flowered plant.

Inheritance in Muskmelon

Since very early times melons have attracted both the professional and the amateur plant breeder. Sagaret (*22*) in 1824, some 40 years before the time of Mendel, made a series of interesting genetic studies with melons. He was undoubtedly one of the earliest forerunners of modern geneticists. His work very definitely shows that he had the idea of contrasting unit characters in his crosses. However, he failed to follow his results into the F_2 generation or to analyze them mathematically. From a cross of two distinctive varieties, Sagaret found that in the F_1 yellow skin was dominant over white skin, netted epidermis over smooth epidermis, pronounced ribbing over smooth ribbing, and acid flavor over sweet flavor.

Lumsden (*16*) attempted to determine the inheritance of the following contrasting fruit characters: Yellow versus green skin color, round versus obtuse-elliptical shape, large versus small seeds, ribbed versus nonribbed, netted versus smooth surface, and large versus small fruit size. He worked with commercial stocks of unknown purity, but they were apparently heterozygous for the characters studied, for he reported segregation into numerous gradations together with the appearance of both parental types in the F_1. No definite conclusions can be drawn from his work. His own conclusions concerning dominance of specific characters are not supported by his data. With the possible exception of skin color, it would appear that all the characters he observed were determined by multiple factors.

Rosa (*21*) has obtained ratios indicating monohybrid segregation of certain characters; that is, the monoecious condition was dominant over the andromonoecious condition; the tricarpellate ovary was dominant over the five-carpellate ovary. In some earlier work, Rosa (*20*) had been able to demonstrate that pollen from different sources has little if any immediate effect on the qualitative characters of the fruit.

As all varieties of muskmelons are notoriously cross-fertile, most of the commercial varieties are highly heterozygous. It is possible to isolate superior strains by selection and inbreeding. These methods have been adopted to stabilize varieties of commercial importance.

A carefully planned inbreeding program at the California station, continued in a few cases to the seventh generation with Salmon Tint, Hale Best, Honey Dew, Honey Ball, and Casaba varieties, has clearly demonstrated that no deleterious effects result from this amount of inbreeding.

Inheritance in Watermelon

Recently a comprehensive, systematic breeding program at the California station has produced much information that will be of value in dealing with problems of watermelon breeding in the future. Besides developing an effective pollination technique, Porter (*18*), has studied the biology of fruit setting in relation to certain environmental factors and has made observations on the effects of inbreeding.

With reference to inbreeding, strains were isolated that were comparatively homozygous for fruit-shape factors and for a number of fruit characteristics—for example, flesh color, texture of flesh, solidity of fruit, etc. Most varieties show no loss of vigor after four to five generations of inbreeding.

In the case of watermelon wilt, the phenomena of resistance and susceptibility are relative. The commercial varieties are as a rule very highly susceptible to wilt; the inedible varieties (as stock citron), on the other hand, are more or less resistant. No variety observed to date seems to be completely immune.

Rosa (*21*) found that the majority of watermelon varieties are monoecious and a few varieties are andromonoecious. Crosses of varieties representing these two types indicated that the difference was monogenic, the monoecious condition being dominant.

Porter and Poole, at the California station, have determined the mode of inheritance of a number of characters in the watermelon. All of the characters investigated gave monohybrid ratios, and there was no evidence of linkage among any of them. Their experiments indicate that (1) in flesh color, red is dominant over yellow; (2) in seed-coat color, black is dominant over white and tan; (3) in fruit-skin color, dark green is dominant over striped and white; (4) in rind, toughness is dominant over tenderness; and (5) in fruit shape, short is dominant over long.

Inheritance in Pumpkin and Squash

The question of whether pumpkins and squashes will cross has always interested amateur gardeners. Considerable confusion has arisen from an imperfect understanding of botanical relationships. There is no accepted basis for distinguishing pumpkins from squashes. Botanically they belong to three species of the genus *Cucurbita*. As popularly classified there are both pumpkins and squashes in all three species.

Castetter and Erwin (*2*) and Erwin and Haber (*7*) have shown that varieties belonging to the same species cross very readily, while those belonging to different species practically never cross in nature. However, cross-pollinating certain varieties belonging to *Cucurbita pepo* with varieties of *C. moschata* has produced partially fertile hybrids. Until recently only sterile hybrids, or complete failure to develop fruits, had resulted from cross-pollinating varieties of *C. maxima* with varieties of *C. pepo* and *C. moschata*. Van Eseltine, at the New York

(State) station, has recently obtained fertile hybrids of reciprocal crosses of *C. pepo* and *C. moschata* and of *C. maxima* and *C. moschata.* Dana, of the Bureau of Plant Industry, in working for curly top resistance in squash varieties, obtained hybrids of *C. moschata* and *C. maxima* that were self-fertile in the F_1 but male-sterile in the F_2. He has backcrossed the hybrid to both parents and obtained fertile backcross progenies.

Early attempts at a genetic analysis of this genus have proved to be practically worthless, chiefly because the investigators were using heterozygous material in their experiments. They underestimated the value of establishing pure lines as a primary factor in securing reliable results in genetic experiments.

The first attempt at a careful genetical analysis of *Cucurbita* was made by Sinnott and Durham (*26*). They used several varieties of *C. pepo.* After being inbred for several generations, the original types were evidently homozygous, as evidenced by their behavior. At this point, using the inbred material, an investigation of the inheritance of certain characters was initiated. From their results the several characters studied appear to be inherited, as indicated in table 1.

TABLE 1.—*Inheritance in summer squash fruits, Cucurbita pepo (after Sinnott and Durham)*

Contrasting characters	Behavior in F_1	Segregation in F_2
Exterior "ground" color.		
White *v.* yellow	White	3 white to 1 yellow (certain crosses produce 15:1).
Yellow *v.* green	Yellow	3 yellow to 1 green.
White *v.* green	White	12 white to 3 yellow to 1 green
Exterior striping:		
White fruits, nonstriped *v.* green-striped.	do	43 white and 9 green-striped.
Yellow fruits nonstriped *v.* white-striped.	White-striped	Complex.
Flesh color:		
White *v.* cream	White	3 white to 1 cream.
Surface:		
Smooth *v.* medium warty	Warty	3 warty to 1 smooth
Smooth *v.* very warty	do	15 warty to 1 smooth
Shape:		
Disk *v.* sphere	Disk	9 disk to 6 sphere to 1 long. Different crosses gave different results. Maybe 1, 2, or more factors involved. In some, the situation is very complex

Sinnott and his coworkers (*27, 28*) have greatly extended this analysis, particularly with regard to the genes governing sizes and shapes in fruits. In general, these characters appear to be determined by numerous factors, so their inheritance is complex and not completely clear. It has been shown that in the cucurbits inbreeding up to at least 7 to 10 generations does not result in a general decline in the vigor of the plants. This behavior is in distinct contrast to that of corn, onions, etc., where inbreeding immediately brings about a decline in vigor.

Hutchins (*11*), at the Minnesota station, has shown in different color types of Hubbard squash (*Cucurbita maxima*) that green is partially dominant to blue. The F_1 was intermediate in color, and the F_2 and backcross populations segregated as for a single factor. Lotsy (*15*) showed that in *C. maxima* exterior fruit-color inheritance

is for the most part complex. In a cross of Turban (a red strain) × Green Hubbard, the F_2 segregated into 3 reddish to 1 green. The dominance of the red was incomplete. In a cross of Turban × Silver Gray, a very wide assortment of colors occurred in the F_2. Lotsy also showed that the Turban character (fig. 2), caused by incomplete enclosure of ovarian tissue by receptacle or torus tissue, is due to two dominant genes. Turban × Green Hubbard gave an F_2 segregation of 15 Turban forms to 1 non-Turban form.

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ONION IMPROVEMENT

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THE onion is used as a food and for seasoning in nearly all countries, and its culture no doubt dates back to very remote antiquity. According to Sturtevant, as reported by Hedrick (*9*),[1] it is—

One of the things for which the Israelites longed in the wilderness and complained about to Moses. * * * Onions were prohibited to the Egyptian priests, who abstained from most kinds of pulse, but they were not excluded from the altars of the gods. * * * They were introduced at private as well as public festivals and brought to the table. The onions of Egypt were mild and of an excellent flavor and were eaten raw as well as cooked by persons of all classes.

ORIGIN, CULTURE, AND USES

BAILEY (*2*) describes eight species of onions cultivated in North America. *Allium neopolitanum* Cyr. and *A. moly* L. are grown as ornamentals. Garlic (*A. sativum* L.) is used mainly for seasoning. The leek (*A. porrum* L.), the Welsh or Japanese onion (*A. fistulosum* L.), and the shallot (*A. ascalonicum* L.) are all used in the green condition. The tops of chives (*A. schoenoprasum* L.) are used for seasoning. *A. cepa* L. is the species cultivated most extensively. Bailey divides this species into several botanical varieties as follows: (1) The extensively cultivated bulbing type of onion propagated by seed; (2) the potato or multiplier onion, which propagates by branching at the base; and (3) the top onion, which forms bulbils in the inflorescence, which are often used for propagation.

Vavilov (*21*) names the middle-Asiatic center, comprising northwestern India, all of Afghanistan, the Soviet Republics of Tajik and Uzbek, and western Tien Shan, as the primary place of origin of the commonly cultivated onion, *Allium cepa*. As secondary centers of origin of this species he lists (1) the Near East, which includes inner Asia Minor, the whole of Transcaucasia, Persia (Iran), and the alpine Turkmen Republic, and (2) the Mediterranean region. For the Japanese onion, *A. fistulosum*, which is cultivated extensively in the Orient, Vavilov gives the primary place of origin as the Chinese center, which comprises alpine central and western China and the adjacent lowlands.

From these centers of origin the onion has spread to all countries where the crop can be grown at some season of the year. Just when the cultivated onion was first introduced into North America is not known, but at present it is cultivated everywhere in this country as a

[1] Italic numbers in parentheses refer to Literature Cited, p. 249.

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home-garden and market-garden crop. Extensive commercial production, however, is confined to special regions.

The early crop for shipment is grown chiefly in Texas, California, and Louisiana from transplanted plants set in the field in late fall and early winter and harvested the following April, May, and early June. The predominant variety is Yellow Bermuda, but Crystal White Wax and Creole are also grown to a considerable extent. These varieties are used for the early crop because they produce bulbs during the time of the year when the days are short. The Bermuda type cannot be stored successfully for more than a few weeks, but Creole is a good storage onion.

The intermediate crop is grown primarily in Texas, New Jersey, California, Oklahoma, Washington, and Iowa from transplanted seedlings and from dry sets, the crop being harvested chiefly during June and July. In Texas the principal intermediate variety is the Yellow Bermuda; in California, the Stockton Yellow Globe and California Early Red; in Iowa, the Yellow Bottleneck; in the East, the Ebenezer, Yellow Strasburg, and others of the same type. In Texas and California the intermediate crop is grown from transplants; in other districts dry sets are used.

The late or main crop, which is produced chiefly in Michigan, New York, Indiana, California, Ohio, Massachusetts, Colorado, Minnesota, Idaho, Oregon, Washington, Wisconsin, and Utah, is usually seeded directly in the field and harvested in August and September. This crop, most of which is stored, supplies the demand from September until late March or April. Storage varieties are not

OFTEN *an onion crop that might have been a profitable one brings the grower a loss because of unfavorable weather conditions and the occurrence of certain insect pests and diseases that take their toll in both field and storage. Smut occurs in practically all of the main onion-growing States of the North, while pink root is present in most of the onion districts of the South and West. Onion thrips are always present on both the bulb and seed crop. Smudge, neck rot, and other diseases take an additional share of the crop after harvest. Other losses occur because of premature seeding in the field and sprouting in storage. Until very recently, little has been done to alleviate these difficulties by scientific breeding methods. Present researches and experiments, however, make the possibility of preventing many such losses by developing superior varieties of onions more and more promising. In most cases resistant varieties and strains have been found, and in some cases promising hybrids have been produced and are under test.*

the same for all sections. In California, Australian Brown is used; in Oregon, the Oregon Danvers; in the Rocky Mountain States, Sweet Spanish and Mountain Danvers, and in the Northern States from Minnesota to Massachusetts, the yellow globe type such as Yellow Globe Danvers, Southport Yellow Globe, and Ohio Yellow Globe. Other varieties stored to some extent are Southport Red Globe, Southport White Globe, Red Wethersfield, White Portugal, Ebenezer, and Yellow Strasburg. With the exception of Sweet Spanish, these storage varieties are rather pungent.

During seasons of low production imports have been chiefly from Spain, Egypt, Chile, Italy, and Canada.

The quantity of onions consumed per capita in the United States is fairly constant regardless of price. During years of overproduction a portion of the crop is usually plowed under, and during years of underproduction imports are increased. The onion market is not very elastic, oversupplies are not readily absorbed, and consequently it is rather easy to have overproduction. As a rule, onions are used by most families in comparatively small quantities but fairly constantly throughout the year for seasoning, in salads, and as a main dish cooked in a variety of ways. Onion salt is also being manufactured in considerable quantities for use in catsup, chili sauce, soups, and sausage. But while the quantity of onions consumed per capita is not large, the total amount used gives this crop a commercially important place among the vegetables. The average onion acreage for the United States during the 5-year period 1928–32 was 84,430 acres, with a production of 13,247,000 100-pound sacks, giving a yearly return to the producers of approximately $17,353,000.

VARIETAL ADAPTATION

Among the onion varieties grown in the United States there are many types differing in size, shape, and color of bulbs, pungency, keeping quality, time of maturity, and tolerance to diseases, insects, sunscald, and high and low temperature. It has been necessary to maintain a considerable number of varieties, partly because of consumer demands relating to season and use, but chiefly because of the different environmental conditions under which the crop is grown. The storage onions of the North, for example, do poorly in the South, and the extra early varieties commonly grown in the South are ill-suited for production in the North.

The adaptability of varieties to certain regions, according to Magruder and Allard (*14*), is often determined by length of daylight, called the photoperiod. The time when bulbing is initiated is determined by the length of the photoperiod and not by the age of the plant, and the minimum photoperiod necessary to initiate bulbing varies with different varieties. The investigators named above were able to group the varieties into classes according to the minimum photoperiod required to produce 100 percent normal bulbs as follows: 12 hours, Yellow Bermuda, White Creole, and Early Grano; 13 hours, California Early Red, Yellow Strasburg, Ebenezer, and Yellow Danvers Flat; 13.5 hours, Early Yellow Globe, Mountain Danvers, Ohio Yellow Globe, Australian Brown, White Portugal, Southport Yellow Globe, and Sweet Spanish strain no. 1; 14 hours, Red Wethersfield,

Southport Red Globe, and Italian Red; 14.25 hours, Yellow Globe Danvers; normal day (maximum of 14.9 hours), Sweet Spanish strain no. 2. Most commercial varieties are not homozygous or pure for the genes that determine the minimum photoperiod for bulbing, so there may be some plants that bulb at a shorter photoperiod than is characteristic for the variety.

Early maturity, according to Magruder and Allard, seems to depend on the ability of the plant to start bulb formation at short photoperiods and to proceed very rapidly with the process after the minimum period for bulbing is reached. In the North it is almost impossible to secure good yields of the extra early varieties like the Bermudas, Early Grano, and Creole by sowing seed directly in the field, because seeding is usually done at a date when the length of day has already passed the minimum for bulbing. Consequently the plant develops only a few leaves and a small bulb. To secure large bulbs of the extra early varieties in the North it is necessary to sow seed early in a greenhouse or in a hotbed in order to have large plants before the minimal photoperiod for bulbing occurs.

The late-maturing varieties of onions usually do poorly in the South, chiefly because the photoperiod required for bulbing comes during hot weather, when sunscald, thrips, and pink root combine to retard the growth of the plant. Lateness of maturity, according to Magruder and Allard, may be due to a long photoperiod requirement, to a slow rate of bulb development after the minimum occurs, or to a combination of the two. Sweet Spanish, a late variety, is able to produce fair crops in the South because it is somewhat resistant to sunscald, thrips, and pink root.

In central California there is a considerable acreage of the so-called intermediate crop of onions. The seed is usually sown in field beds in late August and the seedlings are transplanted in late November and December. During the winter and early spring the plants usually make a large vegetative development. Bulbing does not begin in the spring until the hours of daylight reach the minimum for the varieties in question. For this crop, varieties such as Stockton Yellow Globe, California Early Red, and Italian Red are used. If the late varieties of the North or the early varieties of the South are used they make a good vegetative growth, but in the spring the plants form seed stems instead of bulbs.

These few points regarding adaptation are brought out to show why a variety may do well in one district and be worthless in another. Sweet Spanish is much more widely adapted than many varieties because of its resistance to high temperature conditions and to certain insects and diseases. Other varieties will be more widely adapted when plant breeders incorporate in them genes for resistance to diseases and insects and others that permit them to grow under a wider range of climatic conditions.

INTRODUCTION OF PRESENT COMMERCIAL VARIETIES

It is difficult to obtain authoritative information on the method and time of introduction of the older important commercial varieties. the first mention in seed catalogs of certain important varieties is as follows: Silverskin (White Portugal), 1810; Crystal Wax, 1901; Red Wethersfield, 1849; Ohio Yellow Globe, 1901; Southport Red

Globe, 1889; Southport White Globe, 1889; Southport Yellow Globe, 1888; Yellow Danvers (Flat), 1866; and Yellow Strasburg, 1844. According to Morse (*17*), the variety Australian Brown was introduced into North America from Australia in 1894, under the name of Brown Spanish, but later was renamed by W. Atlee Burpee. An improved strain, Australian Brown U. C. No. 1, was introduced by the California Agricultural Experiment Station in 1935. Sweet Spanish seed was secured by the United States Department of Agriculture from Luis Tono, American consul in Spain, in December 1908, under the name of Denia, and was distributed to seedsmen and several agricultural experiment stations. An improved strain, Sweet Spanish Colorado State No. 6, was introduced by the Colorado Agricultural Experiment Station in 1936. According to Morse (*17*), Prizetaker was first offered to the trade in America by William Henry Maule in 1888, from seed grown by C. C. Morse the preceding year at Santa Clara, Calif. In Europe this variety was known as Spanish King. The Early Grano onion, named and introduced by the New Mexico Agricultural Experiment Station (*8*), was secured from Spain in 1925 under the name of Valencia Grano by the Barteldes Seed Co., of Lawrence, Kans.

Morse (*17*) states that the California Early Red has been developed from the Red Italian Tripoli. The latter was probably brought to California by the early Italian emigrants before 1900. An improved strain, California Early Red, U. C. No. 1, was introduced by the California Agricultural Experiment Station in 1935. The variety Stockton Yellow Globe was originated by a number of American and Japanese growers in California in response to a demand for a nonbolting yellow globe onion; consequently there are a number of strains of this variety, the type of which has not as yet become definitely established. According to Erwin and Harter (*6*), the parent stock of Yellow Bottleneck was "Birn Zwiebel" and was secured from Germany in the late sixties by a Mr. Lafrenz, of Davenport, Iowa. The Creole variety was probably brought to Louisiana by the early French settlers. Yellow Bermuda (formerly called White Bermuda) was probably introduced from the Canary Islands some time prior to 1901.

VARIETAL IMPROVEMENT

OFTEN an onion crop that might have been a profitable one brings the grower a loss because of unfavorable weather conditions and the occurrence of certain insect pests and diseases that take their toll in both field and storage. Smut occurs in practically all of the main onion-growing States of the North, while pink root is present in most of the onion districts of the South and West. Onion thrips are always present on both the bulb and seed crop. Smudge, neck rot, and other diseases take an additional share of the crop after harvest. Besides these, other losses occur because of premature seeding in the field and sprouting in storage. Little has been done until very recently to alleviate these troubles by scientific breeding methods. Hope of preventing many losses in the future by developing varieties resistant to various insects and diseases and certain unfavorable climatic conditions seems more and more promising. Some of the work actually under way is described in later sections of this article.

Commercially Maintained Seed Stocks

To give a comprehensive idea of onion improvement as it is being conducted at present, it will be necessary to review methods employed by commercial interests as well as by State and Federal investigators. Most of the onion seed produced at the present time is grown in California. There the mother bulbs of the different varieties are grown like those for market, with the exception that the rate of planting is heavier so that the plants are more crowded and a somewhat smaller bulb is produced. These are grown by contract at so much per 100-pound bag. Harvesting is usually done in August and September, and the bulbs remain in the bag until time to plant in the field in late November or December. Before planting, most seedsmen pass the mother bulbs over a grading table to sort out the off-color ones and at the same time select mother bulbs of good type to plant for the production of stock seed. As a rule, the bulbs of the various varieties are distributed to ranchers who contract to grow the seed at so much per pound.

If mother bulbs are selected carefully, it is possible to maintain fairly uniform stocks of the different varieties. Onions, however, are highly cross-pollinated, and commercial varieties have a very mixed heredity. Usually there are enough differences between the plants of a variety so that it is possible to select rather widely for type. It is seldom that any two people have exactly the same idea of what the type should be in making selections. As a consequence there are many strains of each variety. Also, by following the selection method exclusively certain recessive colors and off-types are never bred out; they are carried along indefinitely. Progressive seedsmen, however, are beginning to use scientific methods to develop strains that are more uniform in size, shape, and color. Breeding for the development of resistance to diseases and insects, however, is being conducted chiefly by the Federal Government and by the State-supported research institutions. To understand these methods better it is well to know something about the flowering habit and the floral characters of the onion plant.

Inflorescence and Pollination

When mother bulbs are planted in the late fall or winter the rudimentary parts of the flower stalks do not differentiate until the following spring, and it is usually 3 or 4 weeks after differentiation before the flower parts emerge through the sheaths that surround them. The flower stem elongates rapidly and may develop to a height of 5 or 6 feet but usually not more than 3 or 4 feet. The number of flower stems per plant ranges from 1 to 20 or more, depending on the size of mother bulb, the variety, and climatic conditions.

The flowers are borne in simple umbels at the upper end of the elongated stalk, the young buds being enclosed within a papery bract which is split open by pressure of the developing buds shortly before the flowers open. The number of flowers per umbel may range from 50 or less to 2,000 or more. The flowers have six perianth lobes or floral leaves in two whorls of three each and six stamens in two whorls of three each. The pistil has a three-celled ovary with two ovules in each cell. The anthers of the three inner stamens are the first to open, shedding their pollen one after the other at irregular intervals,

after which the anthers of the outer whorl of stamens open, also at irregular intervals (fig. 1). The pollen of a single flower is shed before the stigma becomes receptive, and the process is usually completed in 24 to 36 hours. The style is approximately 1 mm (0.039 inch) long when the flower first opens, not reaching its maximum length of about 5 mm (0.197 inch) until a day or two after all the pollen from that flower has been shed. The flowers of a single head may continue to open over a period of 2 weeks or longer, and a plant may be in flower for 30 days or more.

Most of the pollen is shed between 9 a. m. and 5 p. m. Pollination is effected mainly by insects that go from flower to flower and visit the nectaries at the base of the three inner stamens. Interpollination among flowers of the same umbel is no doubt of frequent occurrence, as the same insect has been observed to visit many flowers on an umbel before leaving. In the onion, however, cross-pollination is the rule.

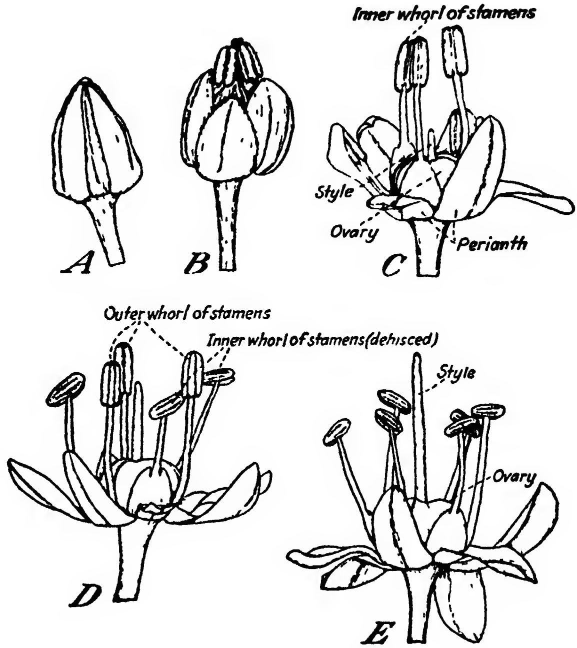

Figure 1.—Method of flower opening and pollen shedding in the onion: *A*, Flower bud just before opening; *B*, the two outer whorls of floral organs expanding and the inner whorl of stamens elongating; *C*, just before the shedding of the pollen by the inner whorl of stamens; note the short style; *D*, the three stamens of the inner whorl have shed their pollen and the three of the outer whorl have elongated; *E*, all six stamens have shed their pollen; note the long style, now receptive. (From Jones and Rosa, *Truck Crop Plants*.)

Selfing an Aid in Onion Breeding

In the onion selfing or inbreeding, accomplished when a plant is self-pollinated, is not an end in itself but merely one of the tools used in the breeding program. Inbreeding in the onion is almost always accompanied by a loss of vigor for a number of generations. However, it permits many undesirable characters that have been carried along in the germ plasm, perhaps covered up by dominant traits, to express themselves, so that the lines possessing them can be rogued out. The main purpose of inbreeding is to develop lines that will breed true for certain characters. Selfing is accomplished in the onion by covering the entire umbel to prevent contamination with foreign pollen. When the first flower opens on an umbel the entire inflorescence is enclosed within a 1-pound manila

paper bag and tied closely so that there will be a crowding of the flowers within the bag (fig. 2). If the umbels are small, as is usually the case after several generations of inbreeding, a number of heads can be enclosed in the same bag, thereby crowding flowers and facilitating pollination. Once each day toward evening, when the pollen is dry, the bags are tapped rather vigorously to help circulate the pollen within.

Breeding Program with Inbred Lines

Much of the improvement work, especially by commercial seedsmen, has as its object the freeing of varieties from plants that are off-type and making a variety or strain uniform for important commercial

Figure 2.—Method of self-pollinating onions. Inflorescences are enclosed in 1-pound manila paper bags.

characters. This can best be done by selecting bulbs that are true to type, selfing to secure uniform and true breeding lines, and finally massing the apparently similar selected inbred lines to bring about crossing, which will restore vigor. Such a program follows:

First year.—Select a large number of commercial bulbs that approach the ideal for the variety; the larger the number the better the chance of securing desirable lines. Plant the selected mother bulbs in late fall, winter, or early spring, depending upon the locality.

Second year.—Self-pollinate as described in the section on selfing.

Third year.—Grow progenies of all selfed plants separately. Destroy undesirable lines during the growing season, or at harvest time, or upon their removal from storage. Retain the best bulbs in 25 or more of the most outstanding lines and plant for selfing and open-pollination.

Fourth year.—Half of the umbels on each plant are selfed and the others are allowed to open-pollinate. By following this procedure it is possible to secure a

supply of open-pollinated seed of superior quality that can be increased rapidly to quantity production. For practical purposes it is usually best not to inbreed more than two generations, because as a rule the plant is greatly weakened and it is difficult to secure a quantity of seed.

Fifth year.—Grow the progenies that were selfed in the fourth year separately and again select the best bulbs from at least 25 lines for open-pollination.

Sixth year.—Group all selections and plant them in the field so that the maximum amount of crossing between unrelated lines will occur. Mass the seed and increase.

Use of Flies to Facilitate Crossing

When new characters are to be incorporated in a variety, as is necessary in most cases when breeding for disease resistance, then the breeder must resort to crossing. Plants to be used for crossing are

Figure 3.—Method of introducing flies into small pollination cages. The cages are made of cheesecloth stretched over wire frames and tied at both ends. (Courtesy California Agricultural Experiment Station.)

usually set 2 to 3 feet apart in the row to allow plenty of room for manipulation of the small cage to be described later. The umbels are bagged as soon as the first flower opens. At first only a few flowers on an umbel open daily, but the number increases until full bloom, when 50 or more may open in a single day. These early flowers are removed several times daily from the umbel of the female parent. When the weather is hot they must be removed often because the anthers shed their pollen very soon after a flower opens. When blossoming is at its peak, open flowers are no longer removed but are emasculated and used for crossing. Umbels must be examined frequently and the anthers removed from the open flowers before the pollen is shed to prevent contamination of the umbel.

When enough flowers have been emasculated, the remaining buds of the inflorescence are removed. The emasculated and disbudded umbel is then enclosed under a small cheesecloth cage as shown in figure 3. The inflorescence of the male, or pollen, parent, which has also been kept covered to prevent pollen contamination, is cut off and enclosed within the same cage, with the base of the stalk standing in a bottle of water. When handled in this manner the flowers continue to open and shed pollen for a week or more. Flies are added to the cage to do the pollinating. This technique, as compared with hand-pollination, makes it possible to multiply greatly the number of crosses, and also to secure a higher percentage of seed setting. To be certain that flies are free from foreign pollen, it is necessary to raise them under controlled conditions.

At Davis, Calif., where considerable onion-breeding work is under way, a technique for the growing of flies for pollination purposes has been developed. Lungs of beef, upon which the adult blowflies lay their eggs, are exposed on tables in the open. The lungs are under a roof to provide protection from a high temperature and rain, which might kill many of the larvae. Within a few days the larvae hatch and begin to feed. When mature they begin to wander about to find a place to pupate, at which time they are trapped by attaching a trough along the side of the table into which the larvae fall. A pail, containing a small amount of finely screened sand, is suspended at the end of the trough. Once each day the pail is removed and replaced by another so that each pail will contain larvae of approximately the same age. The larvae soon burrow into the sand to pupate, and later the pupae are separated from the sand by screening. The pupae are held at room temperature and are placed in a small screen cage before the adults emerge (fig. 3). Each cage, measuring about 6 by 6 inches, has a cone-shaped top, at the apex of which is a small opening closed by a cork. As the flies hatch they gradually move up into the cone. When used in pollinating, the cone is inserted into the lower end of the cloth cage containing the two umbels, the cork is removed, and as many flies as needed are allowed to escape into the cage. They soon begin to feed and in doing this carry pollen from flower to flower and accomplish pollination.

It is often desirable to accumulate mature pupae in order to have a good supply on hand for the peak of the pollinating season. They can be kept for several weeks at about 45° F. It is best not to store them at this temperature until the adults are almost ready to emerge, otherwise fewer of them will emerge. Also, the flies appear to be less active when the pupae are stored early in the pupation period.

BREEDING FOR RESISTANCE TO DISEASE

PINK root of onion, caused by the fungus *Phoma terrestris* Hansen, is a major disease in many onion-growing districts, especially of the South and West. Porter and Jones (*18*), working in California, found that Sweet Spanish was slightly resistant to pink root and that the Japanese onion, *Allium fistulosum*, Nebuka type, was very resistant. In California, Australian Brown No. 17, a single plant selection, is somewhat more resistant than the commercial variety from which it was isolated, and Sweet Spanish No. 35, another single plant

selection, is also more resistant than the commercial variety. Felix (*7*) has also reported that Winterhecke and White Welsh, varieties of *A. fistulosum*, as well as different strains of Nebuka (Natsu-negi Nebuka, Senj-negi Nebuka, Tokyo-Nebuka, and Iwatsuki), are resistant to pink root.

The various types of *Allium fistulosum* have little commercial importance in the United States, but it would be desirable to have certain insect- and disease-resistant characters they possess incorporated in varieties of *A. cepa*. With these objects in view, Emsweller and Jones (*3*) have made a large number of crosses between some of the Nebuka types and many varieties of *A. cepa*. First-generation hybrids of Yellow Globe Danvers × Nebuka and Nebuka × Australian Brown have been grown on soil heavily infested with the pink root organism; the roots showed some pink, but the plants apparently were not checked in their growth. The Australian Brown variety has proved very susceptible to pink root, yet the hybrid grew vigorously on infested soil throughout the season. Back crosses have been made to the Australian Brown variety, but readings have not as yet been made on resistance.

The smut disease, caused by the fungus *Urocystis cepulae* Frost, is present in most of the onion-growing districts of the North. Formaldehyde applied in the row at time of seeding is a satisfactory control measure, but the cost of this treatment could be eliminated by the development of resistant varieties. In 1925 Anderson (*1*) suggested the use of Winterhecke as the logical parent for the breeding of a smut-resistant onion by crossing. He states that it is almost immune to smut, and by his description of the variety one is led to believe that it is the Nebuka type of *Allium fistulosum*. In 1932 the writer sent seed of the Nebuka to A. G. Newhall, of Cornell University, who tested the seedlings under epidemic conditions and found them to be practically immune to smut. Breeding work is under way at present looking toward control by the use of resistant varieties. Progenies involve crosses between the two species, *A. cepa* and *A. fistulosum*. Only a few first-generation hybrid plants were secured, and these have been self-sterile. Back crosses have been made to both parents, however, but as yet these progenies have not been subjected to resistance tests.

Mildew, caused by the fungus *Peronospora schleideni* Unger, is one of the most destructive diseases to the onion seed crop. In California losses may run as high as 80 percent in some seasons. Several onion strains that are highly resistant to mildew have been isolated by investigators of the California Agricultural Experiment Station. One of these is a male-sterile strain of Italian Red, pedigree 13–53, the leaves of which are highly resistant and the seed stems apparently immune. Many progenies are now being tested under epidemic conditions.

A disease called smudge, caused by the fungus *Colletotrichum circinans* (Berk.) Vogl., does considerable damage to the storage crop of the North by causing bulb shrinkage and premature sprouting. Walker, Link, and Angell (*23*) have shown that pigmented varieties of onions are resistant to smudge, while the white are not. On pigmented onions the disease is confined mainly to the neck. Resist-

ance is probably due mainly to the presence of protocatechuic acid—one of the carbolic acids—which is in some way closely associated with the yellow and red pigments in the dry outer scales of the bulb. Insofar as known, this is the first case where resistance to a certain disease has been shown to be due to a definite chemical constituent. Rieman (*20*), in a study of the relation of pigmentation to disease resistance, states that the genes *W* (red) and *Wy* (yellow), which are responsible for the production of the red and yellow pigments, are also responsible for the production of protocatechuic acid. Whether or not resistance can be incorporated in the true-breeding white varieties of onions remains to be determined.

According to Walker (*22*), pigmented onions are also more resistant to the invasion of certain species of the fungus *Botrytis* (*B. allii* Munn, *B. squamosa* Walker, and *B. byssoidea* Walker). He states that resistance in colored bulbs appears to be due to a water-soluble toxic substance in the outer scales that excludes the fungi. Colored bulbs are not resistant once infection is established.

Yellow dwarf is a virus disease of onion that causes a characteristic yellowing, wrinkling, twisting, and drooping of the leaves and dwarfing of the plant. This disease was prevalent for a time in the Pleasant Valley onion district of Iowa and has also been reported in other districts. In a field test of 34 varieties in 1929 Henderson (*10*) found that Sweet Spanish was the only variety showing marked resistance. Plants of this variety did not contract the disease when inoculated artificially and furthermore did not carry the disease in a masked form. It will be recalled that this same variety carries considerable resistance to thrips and to pink root.

BREEDING FOR RESISTANCE TO INSECTS (THRIPS)

THRIPS are present wherever onions are grown, and it is estimated that they cause more loss than all other insect pests and diseases combined. Satisfactory chemical control has thus far been impossible, because a large number of thrips are always protected between the inner leaves of the plant, the pupal stage is spent in the soil, the species is very prolific, the generations overlap, natural parasites are lacking, and other host plants are numerous. The unsatisfactory control secured by chemical means necessitates a mode of attack different from that made in the past. Jones, Bailey, and Emsweller (*11*) showed that certain varieties and species of onion have definite resistance to thrips. Among the most resistant are White Persian, Nebuka, California Early Red, Early Grano, and Sweet Spanish. Counts made in 1932 and 1933 showed that the varieties used were resistant in about the same order in both years, so that certain of their characters evidently influenced the size of the thrips population per plant.

The White Persian variety (P. I. 86279), obtained from Persia through the Division of Plant Exploration and Introduction of the Bureau of Plant Industry, showed by far the most resistance (fig. 4). The resistance of this variety seems to be determined by certain growth characters, which help to hold the thrips population to a minimum, and perhaps by anatomical and physiological characters, which help the plant to withstand injury. The shape of the leaves is probably of importance in restricting the thrips population. In most

varieties the leaf blades have a flat side; in opposite leaves these sides are face to face and the young leaves are closely pressed together so that the larvae are protected against insect enemies and adverse weather conditions. In White Persian the leaves are almost circular in cross section and protection is reduced to a minimum. The wide angle between the two innermost leaves, especially in the young plant, is another White Persian character that helps to restrict the thrips population by reducing their protection to a minimum. Still another character, probably of some importance, is the greater vertical distance between the leaf blades, each new leaf extending its sheath farther beyond the one encircling it than in other known cultivated varieties. This habit of growth produces an extremely long sheath column.

Figure 4.- Thrips-resistant onions. The three rows to the left are the variety White Persian (P. I. 86279); to the right are Australian Brown. Note the serious damage done by thrips to the latter variety and the freedom of the White Persian from injury. (From Jones, Bailey, and Emsweller, *11*.)

If commercial varieties of onions had these leaf characters the thrips population per plant would be reduced to a minimum and it would be possible to secure more efficient control by spraying or dusting. The shape and habit of leaf growth in the White Persian help to restrict the number of thrips; other characters help the plants to withstand injury, but these are as yet undetermined. Maughan and MacLeod (*16*) are of the opinion that avoidance of the plant by the thrips, the angle of contact of the leaves, the stage of growth of the plants, the ability of the plant tissues to recover from injury, and probably other influences have a bearing on resistance.

CROSSES BETWEEN SPECIES

THE Nebuka type of *Allium fistulosum* has very little commercial importance in the United States at the present time, but because of its resistance to various diseases, insects, and adverse climatic condi-

tions it has become a valuable source of breeding material. Crosses have been made between Nebuka and various important commercial varieties of *A. cepa* by Emsweller and Jones (*3*), with the object of incorporating certain resistance factors possessed by Nebuka into commercial varieties of *A. cepa*. This species cross is rather difficult to make, but with the aid of flies considerable numbers of first-generation hybrid seed have been produced.

The Nebuka types are nonbulbing; the hybrids between them and *Allium cepa* are intermediate in bulbing habit (fig. 5). Nebuka is a perennial; *A. cepa* is a biennial; the hybrids between the two are perennials, the tops remaining erect and the plants continuing to grow

Figure 5.—*A*, Commonly cultivated bulbing type of onion, *Allium cepa*, variety Yellow Globe Danvers; *B*, Japanese onion, *A. fistulosum*, Nebuka type; *C*, first-generation hybrid between the two. This species cross gives great promise for breeding onions resistant to diseases and other adverse conditions (*3*).

as long as weather conditions are favorable. Although seed is produced in abundance by Nebuka, the plants continue to form divisions at the base, and these can be used for propagation. In date of flowering the hybrids are intermediate between the two parents. Nebuka is usually in bloom 6 or 7 weeks before *A. cepa*. Blossoming occurs irregularly over the entire inflorescence throughout the flowering period in *A. cepa*, but in Nebuka the terminal flowers open first and blossoming proceeds progressively toward the base. In the hybrid the terminal flowers are the first to open, although with less precision than in Nebuka; then a wave of opening extends toward the base, but this does not terminate the blooming of the umbel, for blossoming then continues for a time over the entire inflorescence as it occurs in *A. cepa*. In *A. cepa* the perianth becomes fully expanded; in *A. fistulosum* it remains erect; the hybrid resembles the *fistulosum* parent very

closely. In the Nebuka varieties the leaves are circular in cross section, whereas in most varieties of *A. cepa* the leaf blade is semicircular; in the hybrid the semicircular type of leaf is dominant. Under similar growing conditions the hybrids show more vigor than either of the parents. They multiply rapidly by subdivisions at the base, and should be able to increase and perpetuate themselves under natural conditions. The hybrids are practically self-sterile; they are, however, useful as pollen parents for back crossing to both *A. cepa* and *A. fistulosum*. When the percentage of functional reproductive bodies is very small, normal sperm cells are naturally more numerous than normal egg cells, because of the much larger total number produced.

PREMATURE SEEDING AND FREEZING INJURY

PREMATURE seeding (bolting) occasionally causes heavy losses in the early crop of the South and in those districts where an intermediate crop is grown from dry sets or transplants. In central California the percentage of bolting is high when a cool spring follows a warm fall. A warm fall causes a large plant to develop. This size and cool spring weather provide the proper combination of conditions for bolting, according to Jones, Poole, and Emsweller (*13*). Because of the lower temperatures prevailing along the central California coast, bolting is more prevalent there than in the interior valleys, making it an ideal place to select and breed nonbolting strains that may be useful elsewhere. The difference in bolting habit between varieties is clearly brought out by comparable plantings made in five locations in California during the season 1934–35. A few of the varieties, with the percentages of bolting, follow: Babosa, 73; Lord Howe Island, 66; Earliest Express, 66; Early Grano, 63; Blood Red Rocco, 51; White Italian Tripoli, 42; California Early Red, 19; and Italian Red, 17. A selection out of Stockton Yellow Globe, strain 36–40, gave only 2 percent of bolters, while a selection out of Stockton Yellow, strain 21–1–3–4–S_3, inbred for six generations, was entirely nonbolting. These highly nonbolting strains are being used in crosses to incorporate this character into varieties that are prone to seed prematurely when conditions favor.

Magruder and Hawthorn (*15*) found varietal differences in resistance to freezing injury, the soft-textured types of onion, such as Yellow Bermuda, Crystal Wax, California Early Red, Extra Early Yellow, and Italian Red, being the most susceptible.

GARLIC

THE culture of garlic (*Allium sativum*), like that of onion, dates back to time immemorial. Vavilov (*21*) gives middle Asia as the primary center of origin and the Mediterranean region as the secondary center. From these centers the culture of the plant has become worldwide. It is highly prized for seasoning. Large collections of foreign varieties of garlic have been secured by several States through the Division of Plant Exploration and Introduction. These varieties vary widely in such characters as number, size, keeping quality, color, and pungency of the cloves, time of maturity, yield, resistance to thrips, and extent of flower development. On some varieties flower stems have never

been observed to develop; on others they reach a height of 4 to 6 feet and contain umbels with a thousand or more flowers; and between these two extremes there seem to exist all possible gradations. For some reason, at present unknown, all varieties fail to produce seed. Even on the profusely blooming Spanish and Creole types seeds have never been observed. Because of the lack of sexual reproduction, improvement must be secured entirely through the selection of bud mutations.

CYTOLOGY AND GENETICS OF THE ONION [2]

THE onion has long been used as a source of material for studying the behavior of the somatic and meiotic chromosomes. Emsweller and Jones (*4*) studied the morphology of the chromosomes of the two species *Allium cepa* and *A. fistulosum*, to develop a method by which the chromosomes of a genom could be identified, avoiding so far as possible the use of total chromosome length. Chromosomes were observed at the first division of the microspore, at which time they are well spaced and only one of each pair is present. The length of any individual chromosome when measured in different cells is not constant because of lack of uniformity in stage of contraction and in fixation. The constriction region is assumed to be located at a definite point on the chromosome, making it possible at least at late metaphase to recognize two arms, and a constant index figure can be calculated by dividing the length of the short arm by that of the long arm. Emsweller and Jones (*5*) have shown also that the type of chiasma is gene-controlled. In *A. fistulosum* the chiasmata, at the first metaphase, are localized at the constriction region, while in *A cepa* the chiasmata are placed at random. In the first generation the chiasmata were at random as in the *cepa* parent. In back crosses to *A. fistulosum* chiasmata were localized in 10 plants and at random in 7, indicating that the difference in type of chiasma is controlled by a single gene, the localized type being recessive.

In a genetic analysis of the three bulb colors, red, yellow, and white, commonly present in the cultivated onion, Rieman (*20*) found that it was necessary to postulate five different genes to account for the results secured—*I*, a gene for incomplete inhibition of color; *i*, a gene allowing expression of color; *W*, a gene for red pigment; *Wy*, a gene for yellow pigment; and *w*, a gene for white. The gene inhibiting color, *I*, is dominant to its recessive allelomorph, *i*. The heterozygous factor pair, *Ii*, produces red-necked and cream-colored bulbs in the presence of the color genes *W* or *Wy*. The latter and the factor pair *Ii* are inherited independently. The gene for red, *W*, is dominant to the gene for yellow, *Wy*, and the gene for white, *w*. The color genes are considered to be multiple allelomorphs.

Rasmusson (*19*) observed several abnormalities in chlorophyll development, white, yellow, chlorina, and T-chlorina. The white and yellow seedlings soon die. The chlorina form is yellowish at first but later may become greenish. The T-chlorina is somewhat paler in color than the chlorina and soon perishes. Some green plants when selfed yielded progeny in the theoretical green to white ratio of 15:1. Green and yellow, green and chlorina, and green and

[2] This section is written primarily for students and others professionally interested in genetics or breeding.

T-chlorina in each case occurred in a ratio of 3:1, but in some cases green and chlorina were in a ratio close to 15:1. Green:chlorina:white occurred in the ratio of 9:3:4, as did green:chlorina:yellow.

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BREEDING AND IMPROVEMENT OF PEAS AND BEANS

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PEAS

NATURALISTS have been interested in *Pisum* for several hundred years, and there are many unmistakable references to peas in the writings of the old Greeks and Romans. Columbus is reported to have grown peas on Isabella Island in 1493, and General Sullivan destroyed the growing peas of the Indians in western New York in 1779.

Pickering (*50*)[1] states that of the culinary vegetables *Pisum sativum* is the only kind that can with any certainty be traced back to the Stone Age. It was uncommon for peas to be eaten in other ways than as dry, cooked seeds before 1700.

Much of the history of *Pisum* has been well reviewed by Hedrick, Hall, Hawthorn, and Berger (*14*). Ruellius in 1536 was the first to distinguish between garden and field peas. Since *Pisum sativum* L., the garden pea, and *P. arvense* L., the field pea, are completely cross-fertile, the distinction seems entirely artificial, and most writers now consider both types under *P. sativum*. In addition some varieties of garden and canning peas (unquestionably *P. sativum*) are used extensively for field peas.

It is noteworthy that peas were the first crop with which controlled breeding work for the production of new varieties was begun, and also that they were the crop with which Mendel conducted his historic experiments, which were the beginning of the modern science of genetics.

Vavilov (*80*) indicates that peas probably had their origin in Ethiopia, with secondary centers of diversity in Mediterranean Europe and in southwestern and central Asia. Although many forms are known in the Mediterranean region, peas have never been of much importance in that area. Farther north, in England, peas have reached their greatest perfection, and they are an important crop in Scandinavia, Germany the Netherlands, and France. The Union of Soviet Socialist Republics at the present time probably surpasses all other countries in the production of peas, mostly dry edible seeds. In 1929 the acreage of peas for grain in the Union of Soviet Socialist Republics was 1,435,750 acres. The estimated crop for 1931 was 2,750,000 acres.[2] Further increases are anticipated. The United States pea acreage for all purposes probably does not exceed 1,000,000 acres.

[1] Italic numbers in parentheses refer to Literature Cited, p 277

[2] Communication from R K Bonnett, Moscow, Idaho, 1931

The pea is a vegetable easily introduced in most places where the climate is favorable. The plants of many varieties are cold-hardy and will survive a winter under a snow covering. If slightly frozen they will put out new shoots when the weather becomes warmer. The blossoms are not particularly cold-tolerant and will survive only a light frost. Peas do not thrive very well in warm weather, so their culture in the southern and southwestern United States is confined largely to the winter and spring months. In the southern part of the Union of Soviet Socialist Republics, where summer quickly follows winter, peas are grown to a limited extent. In the north-central part of the Union of Soviet Socialist Republics, east of Leningrad, west of Moscow, and in southwestern Siberia they are a very important crop.

Peas may be divided into at least five classes according to use: (1) Forage or green-manure crops, (2) dry, edible seeds, (3) market-garden or green shelling peas, (4) canning peas, and (5) edible-podded peas, which have no lining membrane in the pod, a condition that has been traced to two genes. The Union of Soviet Socialist Republics and the southern United States devote large acreages to forage and green-manure crops. Nearly all the important pea-producing countries devote large areas to the production of seed for food and feedstuffs, especially the Union of Soviet Socialist Republics, Germany, the Netherlands, and the area around Spokane, Wash., in the United States. Classes 1 and 2 above are usually referred to as field peas. California produces more than two-thirds of the market-garden or truck peas grown in the United States, of which the annual acreage is now well over 100,000 acres.

The climate of England is especially favorable to the production of large-podded market-garden peas of high quality.

Lately the preservation of shelled green peas by freezing has become important in some parts of the United States, particularly the Pacific Northwest. This industry uses both market-garden and canning varieties, but several seedsmen are now working to develop varieties especially adapted to freezing.

THE *most highly evolved pea variety so far produced by breeders is probably Laxton's Progress. It has a very dwarf vine with a zigzag stem, which makes it sturdy and upright; dark-green foliage; and large, straight, dark-green, pointed pods, from which the peas can be shelled readily. Each of these characteristics is important to growers and each received attention in breeding. The most notable characteristic of Progress, however, is that it begins to bloom at the eighth or ninth node on the stem. This may not seem significant to the inexperienced, but to pea farmers it is worth years of difficult breeding work; for it means that Progress is a few days ahead of its nearest rival in excellence, Hundredfold, which does not begin to bloom until the ninth or tenth node.*

The United States cans annually from 12,000,000 to 20,000,000 cases of peas,[3] mainly in the States of Wisconsin, New York, Maryland, Michigan, and Washington. The canning of peas is not an extensive industry in any other country at present. Edible-podded peas are widely grown in continental Europe. They are for the most part more tolerant to heat than are other peas and have now become a rather common vegetable in Hawaii and southern China. In the continental United States they are practically limited to home gardens.

Origin of the Older Varieties

Thomas Andrew Knight, of Downton Castle, Wiltshire, England, the first great hybridizer, began his work with peas in 1787. Some of his varieties are still used, and they have been the foundation breeding stock for most modern pea varieties.

In 1822 John Goss published a paper in which he recognized the dominance of yellow cotyledons and that green segregates from his crosses bred true. If he had carried his observations a little farther he would have antedated Mendel's discoveries by some 40 years.

Succeeding Knight, many famous pea breeders began their work in England. About 1860 McLean, of Colchester, produced Little Gem and his important Advancer, from which the American varieties Abundance and Perfection were derived. Thomas Laxton bred the variety that bears his name, introducing it in 1898. Laxton Bros. later produced Laxtonian about 1907, and Progress in 1921.

Culverwell originated Telegraph, a smooth-seeded variety with long pods and a tall vine, some time before 1877. It became very popular both in England and in the United States. Telephone, a wrinkled-seeded strain of Telegraph, was derived from Telegraph by Carter in 1878, and has largely replaced it, probably on account of its much better quality. Alderman, introduced by Laxton about 1891, has largely replaced Telephone in the United States, probably because of the demand for darker pods.

Several English seed companies have for at least 50 years poured a continuous stream of new varieties into the markets of the world. Most of these have been successful only in England, but such a diversity of varieties has been supplied that most countries find themselves using a number of varieties that originated in England. The principal English seed companies contributing to pea improvement have been Laxton Bros., Sutton & Sons, Carter & Co., and Hurst & Co

All American varieties are undoubtedly similar to English varieties and in many cases confusion exists as to the origin of a given variety. Alaska was introduced as an American variety by A. B. Cleveland about 1880. It is so similar to the English variety Earliest of All, a cross of Ringleader×Little Gem, introduced in 1881 by Laxton, that these two varieties are now indistinguishable. Alaska is a smooth-seeded, very early, straight-stemmed variety with light-green pods and foliage, which typically begins blooming at the eighth node.

Dwarf Telephone as now grown is a midseason variety blooming at about the fourteenth node. The vine is a sturdy dwarf with a zigzag stem, and the pods and foliage are light green. The pods are long and pointed. Introduced in 1888, the variety is now inextricably

[3] A case equals 2 dozen 20-ounce cans.

Origin and Evaluation of New Varieties and Strains

The Wisconsin Agricultural Experiment Station group working with canning peas have greatly influenced the trend in the industry. E. J. Delwiche has been prominent in this work and has contributed at least 11 strains, of which Badger (1921), a variety like Perfection, was the first introduction. Badger is of exceptionally high quality, but the canning trend away from small seeds and susceptibility to wilt has prevented its general use. Horal (1923), a small-vined Perfection type, one of the heaviest-yielding peas known to the canning industry, failed to achieve popularity because of its very decided lack of quality coupled with small seed size. Alcross and No. 19 strains of Alaska have been of value in breeding homozygous wilt-resistant strains of Alaska peas. They are still grown to a considerable extent, and some of the completely wilt-resistant strains of Alaska on the market have been selected from them. Ashford (1924) is an exceptionally good strain of Horsford, but it is later than Perfection, and therefore the demand for it is very limited. Wisconsin Early Sweet (1931) is a vigorous wilt-resistant type approaching Surprise in quality and having the hardiness of Alaska. It promises to become a very important variety. Wisconsin Perfection (1933) has achieved some popularity on account of its hardiness and wilt resistance.

The Canners Seed Corporation has introduced several new strains of peas since 1930. These have all resulted from the breeding work of E. J. Renard. All introductions by this company have been pure (homozygous) for wilt resistance and were bred especially for adaptation to conditions in Wisconsin. Wilt-resistant Perfection (1930), wilt-resistant Alaska (1930), and wilt-resistant Early Perfection (1933) have been very favorably received by the canning trade. The popularity of large-seeded Perfection and Improved Wales will depend on the trend of the canning industry toward or away from large-seeded types

The Washburn-Wilson Seed Co. has introduced several strains of completely wilt-resistant peas since 1932. These are for the most part the result of breeding work carried on by the writer. The most successful of these seem to be Walah (1932), from Prince of Wales; Alah (1932), which is a wilt-resistant Alaska; and Mardelah (1935), a wilt-resistant Surprise type.

C. E. Temple, of the Maryland Agricultural Experiment Station, has originated a strain of Alaska that does well under conditions existing in Maryland and adjoining States. It is resistant to fusarium wilt (caused by *Fusarium orthoceras* Appel and Wr. var. *pisi* Linford) and possibly to certain other diseases.

Stuart F. Smith, of the Sioux City Seed Co., has produced wilt-resistant strains similar to Alaska and Perfection. M. C. Parker, of the Gallatin Valley Seed Co., is breeding peas for fusarium wilt resistance, types for freezing, and types with multiple pods.

It would appear from the emphasis on wilt resistance that fusarium wilt has been of great importance in the United States. To a considerable extent it has been important, even the limiting factor in certain areas. Probably the most interesting thing in connection with the work on fusarium wilt has been the general adoption of pure-

line breeding by the seed companies. It was found that most stocks of partially wilt-resistant strains did not give good canning results, on account of the mixture of prematurely ripened peas from susceptible plants with the normal peas from the resistant plants. After it was found that pure lines were highly satisfactory in the wilt work, pure-line methods were used in connection with other seed stocks, so that the standards of the industry with regard to rogues have been very definitely raised.

Much confusion usually exists in the seed industry as to the exact identity of strains. It is not improbable that some one strain of wilt-resistant Alaska or other varieties may come to be considered of outstanding merit. However, with the lapse of time and the tendency to substitute similar things for each other, confusion will arise as to the actual strain employed. Many companies have found that wilt-resistant Alaska and wilt-resistant Perfection are entirely satisfactory as canning peas and cannot be distinguished in any definite way from corresponding susceptible biotypes except in reaction to wilt, so that they feel justified in carrying only one strain of each major variety. New York State apparently does not have a wilt problem, but many of the Alaska and Perfection stocks delivered in that State are wilt-resistant.

The future canning types for this country are rather unpredictable, but it seems likely that early peas with stems like Alaska or Surprise, and later peas with heavier stems like Perfection, will be in demand. Large-seeded strains are being sought for the canning of ungraded "sweets", but so far they have not given entirely satisfactory yields. Resistance to diseases other than wilt, to insects, and to adverse weather conditions all are problems that will be worked on in the near future by plant breeders, and in some cases such work is already under way. Searles, at the Wisconsin Agricultural Experiment Station, is doing some work on tolerance of pea varieties to aphid injuries.

Among the market-garden types, Progress (Laxton Bros., 1921) is the most important variety. Hundredfold (Sutton, 1910) is next in importance. These two varieties have largely replaced similar varieties like Laxtonian, Blue Bantam, Pioneer, and Peter Pan. Giant Stride (Carter, 1916) is now probably third in importance. It has largely replaced Dwarf Telephone and Stratagem in the western United States. As introduced it was quite a variable strain. Asgrow No. 40 and Stridah are pure-line selections from Giant Stride or similar material introduced in 1930 and 1931. Recently the United States Department of Agriculture, partly in cooperation with the California Agricultural Experiment Station, has proceeded with crosses between Giant Stride and Progress in which desirable early Progress and Hundredfold types have been selected for resistance to strains of *Fusarium*.

Seed stocks handled under the name of Alderman consist essentially of two types. One type is true Alderman (Laxton, about 1891) and is extensively grown in home gardens where a variety adapted to trellising is desired, and to a limited extent in commercial market-garden areas. The other type is common in the truck-farming areas of the West and is either Quite Content (Carter, 1906) or a derivation

from a cross of Alderman with Quite Content. The largest pods and most fancy packs of market peas obtained in the United States are made from this second type of Alderman, which really deserves a name of its own. Sometimes it is referred to as long-pod Alderman, or Alderman with some geographic designation. The best way of differentiating between the Alderman types is by noting pod-wall thickness. The old type of Alderman has a thin pod wall and the new type has a much thicker pod wall.

Early Gilbo (Rogers, about 1934) is an exceptionally promising variety midway in season between Hundredfold and Giant Stride. The pods are straight, well-filled, approximately as large as those of Giant Stride, and moderately thick walled.

Gradus, Thomas Laxton, and World Record are popular in certain areas in the eastern United States, but the pods are so small that western shippers do not use them. These are all early, straight-stemmed varieties blooming at the eighth to tenth nodes. Thomas Laxton has blunt pods, the other two have pointed pods.

Many American seed companies have contributed to the introduction or breeding of superior varieties and strains of peas. Among these should be mentioned Associated Seed Growers, Inc., and their predecessor firms, the Everett B. Clark Seed Co., the John H. Allan Seed Co., and N. B. Keeney & Sons; the Ferry-Morse Seed Co. and their predecessor firms, D. M. Ferry & Co. and C. C. Morse & Co.; the Rogers Bros. Seed Co.; the Washburn-Wilson Seed Co.; the Gallatin Valley Seed Co. and its predecessor firm, the Davis Seed Co.; the Canners Seed Corporation; the Sioux City Seed Co.; W. Atlee Burpee & Co.; the Jerome B. Rice Seed Co.; Francis C. Stokes & Co. and their predecessor firms; the Chas. H. Lilly Co.; the Livingston Seed Co., and Vaughn's Seed Store.

SNAP BEANS

History and Use

Beans (*Phaseolus vulgaris* L.) were introduced from the Americas to Europe and Asia, where they early became popular. They were mentioned in Europe about 1542, and by 1616 a large number of varieties of different types were described. Hedrick, Tapley, Van Eseltine, and Enzie (*15*) have given a very satisfactory summary of the early history of beans and descriptions of varieties now grown or once grown in the United States. The most extensive previous studies of bean varieties were made by Irish (*17*), Tracy (*77*), and Jarvis (*18*).

Beans may be divided into three major classes according to form in which they are harvested and used—(1) dry shell, (2) green shell, (3) snap or green beans. There is some overlapping of these groups. For instance, Canadian Wonder is thought of as a dry shell bean in this country but is considered a good snap bean in parts of the British Empire. Low Champion as used falls in all three categories. Snap bean varieties may be further divided into (a) market garden, (b) home garden, and (c) canning beans, but distinctions on such a basis are not particularly valid, since most of the canning beans are frequently used for the other two purposes. Most of the present discussion will be concerned with snap bean varieties and their development.

Beans are also classified according to type of vine and pods. A bush bean is a type in which the inflorescence is at the tip of the plant; when it appears, the plant stops growing. In a pole bean, on the other hand, the flowers are along the stem, which continues to grow indefinitely, its ultimate length depending on environmental conditions. All bean pods are green when they are very small, but some turn white, yellow, or crystal [4] as they approach an edible stage. The latter types are called wax beans. Pole beans are mostly used for home gardens. Wax beans are everywhere less popular than green, but they are used for canning, shipping, and home gardens. Since wax pods readily show spots, there has been some discrimination against them in sections where pod-spotting diseases are common. From a shipper's standpoint beans are also classified as flat or round. Beans heart-shaped or oval in cross section are usually classed with the round group, and any pod with a diameter in one direction less than 80 percent of the diameter at right angles to it is considered flat.

At the present time Florida produces well over half the shipping crop of market-garden snap beans. New York, Maryland, Wisconsin, Michigan, and Colorado produce a large part of the crop for canning.

Origin of the Older Varieties

An interest in early bean varieties with stringless pods gave the initial impetus to American bean breeding about 1890. Previous to that time seed companies had given but scant attention to bean breeding, apparently being content to introduce a selection made by a farmer or a variety that had become common in some farming community. White Kidney (shell), Dutch Caseknife, Lazy Wife (pole), Early Yellow, Six Weeks, and Mohawk go back too far in horticultural history to be traced with any degree of certainty. Wax beans seem to have been introduced from Europe when Algiers (wax pole) was brought to this country, and German Black Wax (bush) was introduced about 1865.

Even after seed companies became interested in improvement work it was confined mostly to selections from existing stocks or to developing progenies from chance crossings. The seedsmen were seeking early varieties with less fiber in the pod walls and a reduction or elimination of strings as well as a certain smoothness of pod, and in some cases they considered an increase in pod size important. However, these seedsmen gave only incidental attention to offtypes appearing in their stocks, and progress was not very rapid.

The most successful of these early plant breeders was Calvin N. Keeney, of Le Roy, N. Y. Among his productions are Pencil Pod Black Wax, Brittle Wax, Rustless Golden Wax, Wardwell Wax, Burpee Stringless Green Pod, Surecrop Stringless Wax, Giant Stringless Green Pod, and one strain of Stringless Green Refugee. These varieties were all stringless and of very high culinary quality when compared with such varieties as Early Six Weeks and Mohawk, and they all became popular in spite of the fact that they were not quite so hardy as the older varieties. Brittle Wax has persisted as the most popular wax for canning, and Stringless Green Refugee is still the most satisfactory type for canning high-quality green beans. Pencil

[4] Crystal is the term used to describe a nearly colorless, rather translucent-appearing pod

Pod Wax is of very high quality, but the tendency for the pods to curve has kept it from being a popular garden or shipping bean, and the black seed has prevented it from attaining great popularity as a canner. At the time, however, Burpee Stringless Green Pod was sensationally successful and was grown in most home gardens as well as for canning and shipping. The great success of this one variety stimulated Keeney, as well as other breeders, to continue the development of new stringless varieties, while Burpee Stringless Green Pod remained very popular with home and market gardeners, and Giant Stringless Green Pod became the favorite for an early canning variety for packs of cut beans. Part of Keeney's varieties were introduced by the W. Atlee Burpee Co., part by himself. During the last few years the Keeney stocks have been consolidated with those of two other seed companies incidental to the formation of the Associated Seed Growers, Inc.

D. G. Burlingame, of Genesee County, N. Y., introduced Bountiful in 1898. Other early plant breeders were A. N. Jones, of Le Roy, N. Y.; W. H. Grenell, of Pierrepont Manor, N. Y.; and John Kramer, of Doylestown, Pa.

At the present time the most popular flat-podded, early green snap bean for shipping is Bountiful. There is some competition among early round pods, but Black Valentine (Henderson, 1897), New Stringless Green Pod (Associated Seed Growers, Inc., 1930, from Tendergreen, Henderson, 1922), Full Measure (Henderson, 1906), Burpee Stringless Green Pod, and Giant Stringless are the most popular. Red Valentine, a very old bean of uncertain origin, is still used to a small extent. In some sections Stringless Green Refugee (Keeney, 1908) and 1000:1 Refugee (a very old variety) are still used for late shipping beans. The former is also the most important late canning bean where a high quality pack is desired.

Among the wax beans, Hodson Wax (Harvey Seed Co., 1902) is the most popular late shipper. Webber Wax (1913), Sure Crop Wax (Keeney, 1911), and Davis White Wax (Davis, 1895) are popular early flat waxes for shipping. Brittle Wax (or Round Pod Kidney Wax), Improved Kidney Wax (Keeney, 1906), and Pencil Pod Wax (Keeney, 1900) are the most important of the wax beans for canning

Disease as a Factor in Bean Culture

The ravages of diseases early made it necessary for plant breeders to do additional work on the varieties introduced by Keeney and others after 1890. The three most important bean diseases in this country are caused by organisms that invade the seed tissues, remain dormant in them, start new outbreaks on the seedling plants, and cause losses later. These diseases are anthracnose, bacterial blight, and mosaic.

Anthracnose of beans results principally in dark, sunken spots on the pods, which make such beans unmarketable. In the case of dry shell beans the seed may be discolored. Anthracnose can be eliminated from any stock of seed beans by growing the stock in any of the seed-bean-producing areas west of the Mississippi River, since conditions in such areas are unfavorable for anthracnose development.

Bacterial blights cause water-soaked spots that later throw off a

gray or yellow exudate depending on the blight involved. Bacterial blights can be eliminated by growing in dry-land seed-bean areas, or in certain irrigated districts in Idaho and California.

Mosaic causes a green pattern in the leaf, and in severe cases the leaves may be distorted and the pods reduced in size. Mosaic spreads rapidly from one plant to another, and the symptoms often are not apparent. There is no place known where it is possible to eliminate mosaic from bean seeds by growing in a special environment.

In some cases organisms in the soil (frequently *Fusarium martii phaseoli* Burk.) cause severe injuries to the roots, which may reduce the stand or result in premature ripening, but such diseases are not seed-borne.

The relationship of seed-borne diseases to breeding work with various types of beans can perhaps best be explained by examples. Previous to the moving of the seed-bean industry to the West, anthracnose was the most serious bean disease. At the present time anthracnose is seldom seen in market-garden or canning varieties of beans unless the seed has been saved from an eastern-grown crop. On the other hand, anthracnose is quite common in field beans grown in the East, since most of the seed must necessarily be home-grown. New York grows large acreages of both snap and dry-shell beans, of which the latter are troubled yearly by anthracnose and the former only to a minor extent. New York State has had a vigorous breeding program in effect and has originated several strains resistant to various strains of *Colletotrichum lindemuthianum* (Sacc. and Magn.) Briosi and Cav., the organism that causes anthracnose. There has been no major program by any division of the Federal or State institutions to breed snap bean varieties resistant to anthracnose. Resistance to root-rotting organisms has been studied, but not much has been done to breed for resistance against them.

The Newer Bean Varieties

Productions by Private Breeders

In some cases improved strains not possessing any disease resistance have been introduced. Burpee Stringless Green Pod has been largely replaced by Landreth Stringless (about 1927), but the older name has been retained. The latter undoubtedly was of higher quality, but in some sections home gardeners object that the seed of the new strain does not develop quickly enough. On the other hand, quick seed development is a characteristic that shippers and most city consumers object to.

Giant Stringless, Full Measure, and Burpee Stringless have been losing popularity in competition with New Stringless Green Pod (Tendergreen). This new variety is more resistant to bacterial blights than the other three varieties and yields quite well under a diversity of conditions. It is said to come from an accidental cross of Stringless Green Refugee with Full Measure. It was introduced by Henderson in 1922 as Tendergreen, but was pure-lined, renamed, and introduced by the Associated Seed Growers, Inc., in 1930.

Asgrow Black Valentine Stringless was an introduction by the Associated Seed Growers, Inc., in 1930. It is said to come from a cross of Black Valentine with Pencil Pod Black Wax. It is interesting to

note in this connection, however, that some observers have found white and variegated seeds segregating from this variety. This bean is hardy and of very good quality—in contrast to the poor quality of Black Valentine—and is replacing the old Black Valentine rapidly in many shipping sections.

Stringless Green Refugee is very resistant to bacterial blights but extremely susceptible to common bean mosaic and to many other viruses infecting beans, as described by Zaumeyer and Wade (*95*) and Pierce (*51*). In some sections severe economic losses from common bean mosaic on this variety have occurred.

In spite of the specialized machinery developed for canning beans, snap bean varieties have remained essentially general-purpose varieties. However, in a few cases canning has tended to intensify the importance of certain varieties. Stringless Green Refugee has set a standard that canners have sought in an early variety. Stringless Green Refugee is a late, light-green-podded bean, stringless, essentially free from fiber in the side walls, fine-textured, and with small, straight, nearly round pods. It has been used mainly for packing whole, but any oversized pods are excellent for packing as cut beans. Some canners are not interested in the whole pack and can use a variety that will produce a large yield of beans of only moderate quality. In some sections Full Measure is the favorite. It is early, dark-green podded, stringless, essentially free from fiber in the side walls, medium to coarse in texture, with large pods. Where essentially the same qualities are desired but with lighter pods, Giant Stringless Green Pod is used. Flat beans are seldom canned. In the wax types a white-seeded early wax with the quality of Refugee Green is desired. The nearest approach is Brittle Wax, but canners object to the large eye, which can sometimes be seen in the processed beans.

Bean Breeding by Public Agencies

The United States Department of Agriculture began breeding work in 1922 to produce a Refugee type of bean resistant or tolerant [5] to mosaic. This work was started by Wilbur Brotherton in cooperation with the Wisconsin Agricultural Experiment Station and was later carried on by G. H. Rieman, W. J. Zaumeyer, and the writer. The first introduction was U. S. No. 1 (1933), an early mosaic-tolerant strain intermediate in type between Refugee and Full Measure. It has been favorably received in limited areas only and will probably remain of minor importance. The second Refugee type introduced by the Department came in 1935 and is designated U. S. No. 5. All reports on this bean have been very favorable. It is highly resistant to common bean mosaic and tolerant to bacterial blight, and the pods are not distinguishable from Refugee except that those of U. S. No. 5 are free from purple splashing caused by anthocyanin pigment. U. S. No. 1 is from the tenth generation of a cross of Refugee × Wells Red Kidney, and U. S. No. 5 is from a cross of U. S. No. 1 with a mosaic-resistant Refugee rogue. Previous to the introduction of U. S. No. 1 and U. S. No. 5, Rieman, in cooperation with the Wisconsin station,

[5] In this discussion the word "tolerant" is used to describe a variety that suffers no appreciable reduction in yield as a result of infection, although other disease symptoms may be clearly shown. "Resistant" refers to varieties that are apparently unaffected by the disease in any way.

had made fairly extensive tests of No. 536 Canning Wax, which did not prove to be commercially successful but which has since been used in breeding work for mosaic resistance and for quality of pods.

The Wisconsin station began breeding work with Refugee × Corbett Refugee (a rogue type), from which came Wisconsin Refugee and Idaho Refugee, both introduced in 1934. Wisconsin Refugee is about the same in season as Stringless Green Refugee. It is mosaic-resistant, but the type is not so well fixed as Idaho Refugee. Idaho Refugee is about a week earlier than Stringless Green Refugee. It is resistant to common bean mosaic and is being favorably received by the canning trade. The pods carry a slightly heavier purple splashing in both Wisconsin Refugee and Idaho Refugee than in the parent varieties, although there is a possibility of eliminating this by further selection. W. H. Pierce and J. C. Walker introduced these two strains.

The first bean to be bred especially for mosaic resistance was Robust. It is a strain of Michigan Pea bean (dry shell) and was introduced by F. A. Spragg, of the Michigan Agricultural Experiment Station, about 1913 from field selections.

W. H. Pierce and C. W. Hungerford, of the Idaho station, introduced Idaho No. 1 Mosaic Resistant Great Northern about 1930. It is a very hardy dry-shell bean obtained by selection from heterogeneous strains of Great Northern.

Further work on resistance to mosaic in snap beans is being carried on at the Michigan station by C. H. Mahoney and at the New York stations at Geneva and Ithaca.

One of the most interesting developments in connection with canning string beans is the sudden popularity of a strain of White Creaseback known in some places as Blue Lake. This is somewhat different from the ordinary strains of White Creaseback grown in home gardens. The pods are very long, dark-green in color, and round in cross section at a very early stage. Nearly all beans canned from this variety are put up in whole lengths in "asparagus" style. The popularity of this excellent dark bean may mean the beginning of a new era in American bean breeding, since the proponents of light-podded Refugee types can no longer consistently claim that high quality in a canning bean is associated only with light-green pods.

Bean rust is another problem that has required attention during the last few years. Kentucky Wonder and most strains of white-seeded Kentucky Wonder are susceptible to strains of rust. In 1934 L. L. Harter, of the Bureau of Plant Industry, United States Department of Agriculture, introduced U. S. No. 3 and U. S. No. 4 strains of white-seeded, rust-resistant Kentucky Wonder. These were pure-line selections from heterogeneous strains from Europe known as World Wonder and Phenomenon, respectively. U. S. No. 3 has been very favorably received. It is a very early pole bean, coming in bloom only a few days later than Full Measure. The pods are large, round, stringless at all stages, and of high quality. U. S. No. 4 is somewhat later than U. S. No. 3, and the pods are very long, flat, and stringless in early market stages. They represent an improved strain of what would ordinarily be considered white-seeded Kentucky Wonder. Further breeding work is under way involving crosses of

brown-seeded Kentucky Wonder with U. S. No. 3 and U. S. No. 4 and for resistance to other strains of rusts.

In connection with the bean-breeding program of the Department several green and wax canning, market-garden, and pole strains resistant to various diseases are now in the course of development. These are being bred and tested for the most part at Greeley, Colo., Charleston, S. C., and Beltsville, Md. Those now engaged in this work are W. J. Zaumeyer, L. L. Harter, and W. D. Moore in pathology, and the writer and C. F. Poole in genetics. For the last few years S. A. Wingard, of the Virginia Agricultural Experiment Station, has been developing strains of the Kentucky Wonder type suitable for growing in that State and resistant to rust. He has succeeded in establishing very satisfactory late strains that are not early enough for growing seasons in northern or north-central regions.

List of Varietal Introductions

Table 1 shows in a condensed form some of the outstanding bean varietal introductions of the last 20 years or so.

TABLE 1.—*Bean varietal introductions*

Variety or strain	Type	Special characteristics	Introduced by—
Robust	Dry shell (pea bean)	Resistant to common bean mosaic	F. A. Spragg, Michigan, 1913
Idaho No. 1 Great Northern	Dry shell	do	Pierce and Hungerford, Idaho, 1930
Geneva Red Kidney	do	Resistant to strains of anthracnose	Gloyer, 1928
York Red Kidney	do	do	Do.
Virginia Kentucky Wonder	Snap pole	Resistant to rust	Wingard, 1934
U. S. No. 3	do	do	Harter, 1934
U. S. No. 4	do	do	Do.
U. S. No. 1	Refugee	Tolerant to mosaic	Wade and Zaumeyer, U. S. Department of Agriculture, 1933
U. S. No. 5	do	Resistant to mosaic	Wade and Zaumeyer, U. S. Department of Agriculture, 1935
Idaho Refugee	do	do	Pierce and Walker, University of Idaho, 1934
Wisconsin Refugee	do	do	Walker and Pierce, University of Wisconsin, 1934
Corbett Refugee	Refugee rogue	do	Corbett, Sioux City, Iowa, 1931
No. 536	Canning wax	Resistant to mosaic, small pods	Rieman, 1928, U. S. Department of Agriculture and University of Wisconsin
Blue Lake	White Creaseback	High quality dark podded canner for whole length packs	Clear Lake Canneries (?), about 1930
Asgrow Black Valentine	Stringless Valentine	Stringless	Associated Seed Growers, 1930
Tendergreen	Full Measure	Tolerant to bacterial blights	Henderson, 1922
New Stringless Green Pod	do	do	Associated Seed Growers, 1930
Landreth Stringless Green Pod	Burpee Stringless	Refined pod	Landreth, about 1927
Stringless Red Valentine	Red Valentine	Stringless	Landreth, 1930

The development of new disease-resistant varieties of beans has done much to stimulate pure-line work among the seed companies, and many have greatly improved the standards of their basic seed stocks and of the stocks they deliver to canners and to market and

home gardeners. The complex nature of present-day breeding work makes it necessary for seed companies to employ plant breeders with an adequate knowledge of genetics and plant pathology.

LIMA BEANS

ALTHOUGH the botanical differences between lima beans (*Phaseolus lunatus* L.[6]) and common beans (*P. vulgaris*) are not great, it has so far not been possible to cross the two species. The most conspicuous difference is in the flower bracts. They are small, inconspicuous, lanceolate, and pointed in *P. lunatus* and large, conspicuous, and oval in *P. vulgaris*.

Lima beans cannot be grown as far north as common beans. In the South or in the Tropics if a set of blossoms is dropped because of drought or very hot weather, the long growing season still may give plenty of time for beans to be set later. Where the seasons are shorter, failure of the crop may result from the loss of the first blossoms. In California the long growing season makes it unnecessary for the first blossoms to develop into pods.

Limas became popular in the United States after 1824, when seed of the large type—as contrasted with the small-seeded civet or sieva type—was brought from Lima, Peru, by Capt. John Harris, of the United States Navy. It was found that the lima did especially well on the dry lands of southern California. The two limas now most extensively grown are both dwarf varieties, Henderson Bush and Fordhook. Henderson Bush was found along a roadside in Virginia by a Negro laborer about 1885. He sold it to T. W. Wood & Sons, of Richmond, who later sold the stock to Peter Henderson. It is a small erect bush type with very small, flat seeds. It can usually be counted on to produce a crop even under adverse conditions. Wood Prolific Bush, a later selection from Henderson Bush, is a slightly larger plant. U. S. No. 2 lima (1933) is a selection from Henderson Bush developed especially for uniform maturity of the pods on the individual vine. It is not distinct enough to constitute a variety, but under some conditions it may be from a few days to 2 weeks earlier than most strains of Henderson Bush. Henderson Bush and related types are grown to some extent in home gardens but are more generally used for commercial canning.

Canners have wished to combine the hardiness and yield of Henderson with the quality of Fordhook. In 1934 the McCrea Seed Co. introduced the McCrea lima, which is green-seeded when mature, of high quality, but late and not an especially good yielder in eastern canning districts. The green seed character is not apparent in either Henderson or Fordhook, so it is probable that the parentage is some large, green-seeded variety crossed with Henderson.

Fordhook, a large-seeded dwarf plant, was discovered in a field of Challenger pole limas by Henry Fish, of Santa Barbara, Calif., in 1903. Burpee introduced it in 1907. It is now the favorite market-garden variety. A small quantity is canned, but its popularity for canning has not been great because of its sensitiveness to adverse weather conditions.

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[6]In ordinary botanical usage *Phaseolus lunatus* is the civet or sieva bean and *P. lunatus macrocarpus* Benth. the lima bean.

During the last several years the California Agricultural Experiment Station has introduced strains of a very hardy, high-yielding, small-seeded lima known as Hopi, selected by Mackie from limas grown by the Hopi Indians. Most of the Hopi and Henderson Bush grown in California are used as dry, edible beans.

A very noteworthy fact about lima bean breeding is that practically all varieties have arisen by selection and very few from controlled breeding work. Roy Magruder, of the Bureau of Plant Industry, is at the present time carrying on considerable breeding and genetic work involving seed-coat colors, seed sizes, and the breeding of various types for canning.

In the southern United States pole limas with either colored or white seeds are grown extensively in home gardens and to some extent for marketing under the name of butter beans. These are very hardy varieties and probably offer worth-while breeding material for crossing with nonhardy, high-quality varieties such as Fordhook.

GENETICS OF PEAS AND BEANS [7]

Peas

THE many stable forms of *Pisum sativum* early attracted the attention of those interested in theoretical scientific work as well as the attention of many breeders. It was with garden peas that Gregor Mendel in 1856 began his historic experiment, which laid the foundation for genetic science. His findings were made public in 1865 but attracted no attention until they were rediscovered by Correns, De Vries, and Tschermak independently in 1900.

Mendel worked with seven different factors: Yellow *v.* green cotyledons, smooth *v.* wrinkled seed coats, normal *v.* fasciated stems, tall *v.* dwarf growth habit, green *v.* yellow pods, parchmented *v.* nonparchmented pods, and the pleitropic factor for colored *v.* colorless seed coats, colored *v.* colorless leaf axils, and purple *v.* white flowers. A pleitropic factor is one that affects many different characters.

In spite of Mendel's success with the plant, peas have not proved to be ideal for genetic studies, and consequently most of the fundamental contributions since his time have been with organisms other than peas. There are probably several reasons for this: (1) Many single-factor differences frequently show wide divergences from a 3:1 ratio. (2) Linkage values may vary sharply from one cross to another. (3) Different classification of phenotypes gives rise to reports of more than 50 percent crossing over. (4) The number of independent factors and groups of factors appears to exceed the number of chromosomes. (5) Peas have proved to be rather difficult material for cytological studies.

Wellensiek (*85*) brought the available data up to date and has worked unceasingly to eliminate conflicts in designations of various factors. Matsuura (*39*) also reviewed and tabulated the literature dealing with *Pisum* genetics. The following lists of factors are taken largely from Wellensiek, with a few modifications by De Haan (*11*) and Winge (*92*). The number of genes listed is 68, but the known number may be in excess of this. In some cases it has been difficult

[7] This section is written primarily for students or others professionally interested in breeding or genetics.

to decide whether some ratios are the result of pleitropic effects of a single gene or the effect of several genes completely linked. Winge gives a table showing certain gene designations made by himself and 10 other authors, including De Winton (*93*), Wellensiek (*86, 87, 88, 89, 90*), Rasmusson (*55, 57, 58*), White (*91*), Lamprecht (*30*), Pellew and Sverdrup (*49*), Sverdrup (*70*), Nilsson (*42*), Kajanus (*21, 22*), H. and O. Tedin (*72, 73*), and De Haan (*11*).

Pisum Factors

A. Basic gene for anthocyanin color of the flower. It also influences indenting of seeds, seed-coat color, marbling of seed coat (except ghost marbling), leaf-axil color, violet and red pod colors.
A_1, crypto purple; A_2, purple dotted flowers; *a*, white.
Ar. Gene for reddening, salmon-pink flowers.
Ap. Apple blossom.
Am. Pinkish-white flowers.
B. Gene for bluing.
Bl, basic gene for wax or bloom; *bl*, waxless (emerald).
Bta, blunt apex; *bta*, acute apex. } Both recessives must be present in homozygous
Btb, blunt apex; *btb*, acute apex. } condition to produce acute.
Cp, curved pod; *cp*, straight.
Cr. Changes crimson to purple in presence of *A*. (Fedotov (*7*).)
Cv. Intensifies anthocyanin color in presence of *A* and *B*. (Fedotov (*7*).)
Cm. Cream flowers. (Fedotov (*7*).)
Em^1, Em^2, normal; em^1, em^2, emergences if both are present.
Ep' } Thickness of seed coat. (Kaznowski (*23*).)
Ep_1 }
Dw, *D*, *d*. Leaf axil ring double, single, absent. (Tedin and Tedin (*72*).)
F. Purple dotting of seed coat I. (Wellensiek.)
F_2. Purple dotting of seed coat II. (Winge.)
Fe, normal pods, fertile; *fe*, split pods, sterile as female. (Sverdrup (*70*).)
Fa, normal stem; *fa*, fasciated stem.
Fu, resistant to fusarium wilt; *fu*, susceptible.
Fl, gray spotting on leaves; *fl*, green leaves.
Fn, one or two flowers per peduncle; *fn*, three or more flowers per peduncle.
G, green cotyledon; *g*, yellow cotyledon. (Nilsson (*42*).)
Gp, green pod; *gp*, canary yellow pod.
H. With *A* gives orange seed coat.
I. Inhibits action of *G*, giving dominant yellow cotyledons.
If, intermediate flowering; *if*, early flowering.
J. In presence of *A*, causes dark-brown seed coat.
K, normal wings; *k*, keeled wings.
Kl. Inhibits coupling between *A* and *Gp*. (Hammarlund (*13*).)
L, L_1, L_2. Genes for wrinkling or dimpling of seed.
Le, Le_1, *le*. Long, very long, and short internodes.
La. Growth-inhibiting factor. (De Haan (*11*).)
Lb. Growth-inhibiting factor.
Lc. Growth-inhibiting factor.
Ld. Growth-inhibiting factor.

(*Le* dominates if *La* or *Lb* is present, but not if the two recessives, *la*, *lb*, are present. Either *Le*, *la*, *lb*, or *le*, *la*, *lb* is slender. 45:15:4 segregation of tall, short, slender in F_2.)

Lf. Retards flowering time caused by *If*; ineffective by itself.
Lo, Lo_1, Lo_2, Lo_3. Genes for seed length. (Kaznowski (*23*).)
M with *Z* gives "ghost marbling" of testa; with both *A* and *Z*, brown marbling.
M_1 to M_4. Genes for susceptibility to mildew. (Hammarlund (*13*).)
Mp. Rusty radicula. (Tedin and Tedin (*73*).)
N, thin pod wall; *n*, thick pod wall.
Nr, normal; *nr*, narrow rogues. (Pellew (*48*).)
O, *or*, *oy*. Green, lemon, gold pods, stems, and foliage.
Oh. Inhibits the expression of red, converts red to bright-brown seed coat.
P. Thin parchmented membrane in pod; *p*, no membrane.

P_1. Purple pod I } Both dominants necessary to make pod purple.
P_2. Purple pod II }
Pa, green pods; *pa*, pale pods.
Pe, normal pods; *pe*, pearl pods.
Pl, dark hilum; *pl*, light hilum.
Pt. Quick growth of pollen tube.
Q, aborted seed; *q*, normal seed. (Wellensiek and Keyser (*90*).)
R, round seed; *r*, wrinkled seed surface.

(*R* is hypostatic to *A*; *r* is epistatic to *A*. In conjunction with genes L_1 and L_2 of Hadfield and Calder (*12*), the following forms may be distinguished: Smooth, $l_1\ l_1\ l_2\ l_2\ RR$; dimpled, $L_1\ L_1\ L_2\ L_2\ RR$; wrinkled, $L_1\ L_1\ L_2\ L_2\ rr$; wrinkled, $l_1\ l_1\ L_2\ L_2\ rr$).

Re, normal leaves; *re*, reduced leaves.
S, seeds free in pod; *s*, seeds clinging together (chenille or brochette).
Sa_1, Sa_2, Sa_3. Genes for number of stomata. (Tavčar (*71*).)
Sg_1 to Sg_4. Genes for seed weight.
Sn_1, intermediate value for node number; sn_1, low value.
Sn_2, increases the value for node number caused by Sn_1; ineffective alone.
St, normal stipules; *st*, reduced stipules.
T, T_1, T_2. Genes for internode number.
Td, leaves dentate; *td*, leaves not dentate.
Tl, tentril leaves; *tl*, acacia (no tendrils).
U, violet seed coat.
Uni, Normal leaf; *uni*, unifoliate.
V, Strong membrane in pod; *v*, thin membrane.
Wb_1. Strengthening gene for wax.
Wb_2. Strengthening gene for wax.
W_2, green foliage; w_2, white variegated.
X. Stipule size. (Brotherton (*1*).)
Y. Stipule size.
Z, colored seed coat; *z*, uncolored seed coat.

As there are many factors influencing flower color, it is perhaps best to illustrate the genetic constitution of some of the many colors that occur. These are given from De Haan (*11*):

Purple	*A A Ar Ar B B Ap Ap Am Am*
Violet	*A A ar ar B B Ap Ap Am Am*
Rose	*A A Ar Ar b b Ap Ap Am Am*
Light purple	*A A ar ar b b Ap Ap Am Am*
Apple blossom	*A A Ar Ar B B ap ap Am Am*
Apple rose	*A A Ar Ar b b ap ap Am Am*
Apple violet	*A A ar ar B B ap ap Am Am*
Pinkish white	*A A Ar Ar B B Ap Ap am am*
White	*a a Ar Ar B B Ap Ap Am Am*

A cross of violet by apple rose results in a purple F_1 with a trihybrid ratio in F_2 of 27 purple : 9 violet : 9 apple blossom : 9 rose : 3 apple violet : 3 apple rose : 3 light purple : 1 expected to have an appearance between apple rose and light purple. According to the above scheme, all those having *aa* are white regardless of the rest of the genetic constitution. A certain white[8] × apple blossom results in an F_2 segregation of 9 purple : 3 apple blossom : 4 white. According to the designations of Fedotov (*7*), *Cm* can produce a cream flower and it is independent of the action of *A*.

In addition to flower color, the genes that have been listed have an influence on color of the leaf axil. Purple and apple-rose flowers are associated with purple axils; pinkish white, with dull-rose axils; violet and apple violet, with violet; rose and apple rose, with rose; and light purple, with light purple. *Dw* produces a two-ring effect in the axils, *D* a single ring, and *d* no ring.

[8] Only the white of the constitution *aaArArBBApApAmAm* will give the ratio cited when crossed with apple rose.

There is considerable variation in the amount of waxiness or bloom on peas. Waxiness is caused by a gene for wax *Bl*, and is intensified by the presence of either W^b_1 or W^b_2 or both.

Two genes (bt_a and bt_b) must be present in the homozygous condition for a pod to have an acute apex. Crosses between strains with blunt pods and those with sharp result in the F_2 either in a ratio of 15 blunt : 1 acute or of 3 : 1, depending on how many of the genes for bluntness were present in the blunt parent. There is at least one other factor influencing pod-apex shape.

The gene *fe* is responsible for a rather peculiar condition in which the developing pods split along the dorsal suture, resulting in the death of the developing seeds.

The fasciated or flattened stem condition is due to a recessive gene, *fa*. This flattened condition results in a terminal inflorescence that superficially resembles an umbel. Some flower stalks may produce from three to seven flowers, while others produce only one or two on the same plant.

Tallness and shortness in pea plants have long been of much interest, and it has been discovered that many factors are concerned with stem length. In some cases simple 3 : 1 ratios of tall to short are obtained in the F_2 generations from crosses of tall with short. In one such cross, however, De Haan (*11*) obtained an F_2 segregation of 45 tall : 15 short : 4 slender. Two recessive genes must be present to produce a slender plant. Gene *Le* is epistatic to *La* or *Lb* but hypostatic to *la* or *lb*. Genes *lc* and *ld* result in a slightly larger short plant designated "short 2." One of the factors for slender is identical with *lc* or *ld*, but it has not yet been determined which.

The edible-podded condition (no membrane) is determined by the recessive gene *p* in the homozygous condition. The factor *V* results in a very strong membrane when acting in conjunction with *P*.

Pt is a theoretical gene for quick growth of the pollen tube. Its presence has never been determined by actual ratios.

Round seeds are dominant to wrinkled, and segregation is by individual seeds. Several genes influence the condition known as indenting or dimpling, and segregation is by plant. A three-factor explanation has recently been given (*12*) of the conditions designated smooth, dimpled, and wrinkled, respectively.

Seed weight is influenced by several factors, the exact number of which has never been determined. Violet flower is sometimes associated with abnormal hilum, which results in low seed weights on plants having violet flowers. Many other factors also probably influence seed weights.

The Gradus rogue (rabbit ear) character (*1*) is a rather unique condition in which very rapid mutation of the recessive gene *x* for normal Gradus type to the dominant *X* (rogue) occurs when these genes are associated together in a cross. While other factors involved in a cross may be segregating as expected, no plants of normal type may be recovered in F_2 or subsequent generations.

Seed-coat colors are also affected by the gene *A* for anthocyanin. Factors *Ar* and *B* have an effect on seed-coat color parallel with their

effects on flower color, but *Am* and *Ap* have no effect on seed coat. The effects of *Pl*, *M*, *F*, *Oh*, *Z*, and *Mp* on flower color are known.

Disease Resistance

Hammarlund (*13*) reported that immunity of peas to powdery mildew was due to the presence of four genes, M_1, M_2, M_3, and M_4. The varieties commonly grown in the United States are all susceptible to powdery mildew, but artificial control methods have been effective in preventing damage by this organism. Neither genetic nor breeding investigations of powdery mildew resistance have been undertaken in this country.

Wade (*82*) reported that resistance to fusarium wilt of peas was due to a single dominant gene, *Fu*. This was slightly linked with *Le*. Extensive breeding work has been carried out by many workers, and

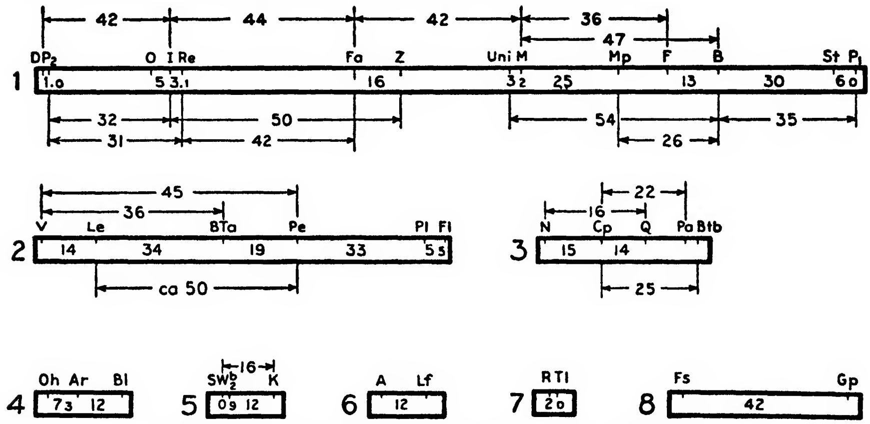

Figure 1.—**Linkage groups in *Pisum*. (After Winge.)**

at the present time all the canning varieties are available in wilt-resistant forms.

Zaumeyer and Wade (*96*) have shown that different varieties of peas show differential reactions to various types of legume mosaics. The presence of many diseases, frequently epidemic in nature, indicates that in the future much work will be done in connection with the inheritance and breeding of disease-resistant strains of peas.

Various reports have shown that many varieties of peas possess some tolerance to the attacks of various root-rotting organisms, but the genetic bases of these reactions have not been determined.

Linkage and Cytology

The contribution of Winge (*92*) on linkage in *Pisum* has greatly clarified the linkage situation. He describes eight linkage groups, which are here redrawn (fig. 1) from his publication.

It is believed that further research will eventually reduce the number of linkage groups to seven, to correspond with the number of pairs of chromosomes known to be present in *Pisum sativum*.

Ring formation (*9*) seems to be the most satisfactory explanation of many of the variable linkage results obtained by Rasmusson, Wellen-

siek, Tedin and Tedin, and other workers. Although Rasmusson (*56*) shows the genetic nature of some linkage intensities, the number of factors involved in the segregation of these intensities is not known. Håkansson (*10*) reports a semisterile condition in association with chromosomal exchange. Sutton (*69*) reports an instance of half disjunction in a case involving four chromosomes.

Beans

The literature on bean (*Phaseolus vulgaris*) genetics and breeding is very extensive. Kooiman (*24*) presents a very thorough review of the subject and does much to clarify conflicts in terminology. Doornkaat-Koolman (*4*) had previously reviewed the literature, especially that dealing with disease resistance. Matsuura (*39*) also presents a summary. Much of the material in this paper is drawn from reviews by these authors, with stress on literature published since 1929.

Inheritance in beans has been investigated for a long time, but there are still many divergent results that need further studies for adequate interpretation. This is especially true with regard to flower colors and their relationship to seed and pod colors.

Shaw (*66*) and Shaw and Norton (*67*) present extensive observations on flower colors, which indicate that at least two factors must interact for the production of pigment in flowers. According to their observations, most varieties with pigmented seeds, with the exception of Red Valentine, have colored flowers. However, many other exceptions to the observations of these authors are now known.

Johannsen (*19*) obtained a dihybrid ratio in progeny from a cross of a white-flowered brown-seeded bean variety with a violet-flowered black-seeded one.

Tjebbes and Kooiman (*76*) explain the results of a spontaneous cross of violet × lilac-flowered, in which dark violet, light violet, lilac, and white flowers appeared in association with red and blue pods and various seed colors on the basis of three genes. *R* causes red pod striping whether or not the ground factor *A* for seed-coat color is present. When *A* is present the flowers are lilac; the seed coat is red, due to *R*. *Bl* changes these colors to bluish tints. Heterozygous *Bl bl* results in light violet. They assumed a total of seven genes for flower color.

Kooiman (*24*) suggested an eight-factor explanation of the various seed-coat colors encountered.

Sirks (*68*) presented a factorial explanation of various seed-coat colors and summarized the literature up to that date.

Lamprecht (*25*, *26*, *27*, *28*, *29*, *31*, *32*, *33*, *34*, *35*) has presented a very satisfactory explanation of most of the seed-coat colors encountered in beans. He assumes eight pairs of genes and the following interactions among them:

P. Basic color factor, in itself producing no color.
C with *P* gives sulphur white; *Cc*, mottled.
J. Pale ecru in seed coat, also in hilum.
G with *PCJB* gives mineral brown; with *PCJV* gives maroon brown; with *PCJBV* gives black; with *Ca* gives caruncle streak.
B with *PCJG* gives mineral brown; when heterozygous with *PCJVv* gives dark dull green; when homozygous with *PCJV* or *PCJVG* gives black.
V with *PCJG* gives maroon brown; when heterozygous with *PCJBb* gives dark dull green; when homozygous with *PCJB* or *PCJBG* gives black.

R. Red.
Ca. Caruncle streak; shows only in presence of G.
PCJ. Chamois color.
PCJG. Blister (yellowish brown).
PCJgB. Golden bronze yellow.
PCJgbV. Violet purple.
PCJGB. Mineral brown.
PCJGV. Maroon brown.

(Chamois, *PCJ*, in the presence *G* and *B* gives mineral brown; *G* and *V* give maroon brown; *B* and *V*, both heterozygous, produce dark dull green; while *B* and *V*, either homozygous or in the presence of *G*, produce black.)

PCJBbVv. Dark, dull green.
PCJBVG. Black.

Micropyle streak is recessive and will not show in the presence of either or both inhibiting factors *Mi* and *Mia;* furthermore, *J* is necessary for its expression even when the inhibitors are absent.

Later, Lamprecht (*33*) has shown that factors *J* and *R* are inherited independently, and that in addition to the *Cc* inconstant marbling there is also *Rr* inconstant marbling.

Schreiber (*64, 65*) explains his results on a somewhat different basis. Genes M_1 and M_2 must both be present to produce a constant marbling effect. *B* is a factor for light brown; *C* is an intensifier. *D* is for dark green, effective only in the presence of the basic color factor *A* or *P*. *L* inhibits partial spotting caused by Shaw and Norton's "*T*". Miyake, Imai, and Tabuchi (*41*) found all seedcoat colors hypostatic to black.

Tschermak (*78*) suggested two genes for eye pattern:

(1) $z_1z_1Z_2Z_2$. Seeds having half or more of the testa pigmented with sharp limits.
(2) $z_1z_1Z_1z_2$. Seeds having half or less pigmented, without sharp limits.
(3) $z_1z_1z_2z_2$. Pigment confined to a small hilum spot.

Sax (*60*) found in his crosses of two types of Yellow Eye beans that the heterozygous condition resulted in a pigmented area exceeding twice that of the parents. Only a single gene was involved.

Currence (*3*) found two distinct types of bean pod stringiness, one due to two dominant complementary genes, the other to an incompletely dominant gene for stringlessness with an inhibiting factor. Joosten (*20*) distinguished 10 classes of stringiness. Prakken (*53*) found 15 stringless to 1 stringy in an F_2 generation.

Tschermak (*78*) observed 3:1 and 13:3 ratios in F_2 for nonconstricted versus constricted pod. Lamprecht (*26*) interpreted his results on the basis of four factors.

Emerson (*5*), Lock (*36*), Doornkaat-Koolman (*4*), and Tschermak (*79*) found green pods dominant over yellow (wax) with a 3:1 ratio in F_2. Currence (*3*) found two factors to determine the difference between these characters.

Tschermak (*79*) found a single factor difference between round versus flat, with round dominant. Wóycicki (*94*) and Currence (*3*) found several factors involved.

Miyake, Imai, and Tabuchi (*41*) have studied the inheritance of color of stem. Two types of green crossed together gave a red F_1, followed by a segregation of 9 red : 7 green in F_2. Pink × green gave 9 red : 3 pink : 4 green.

Emerson (*5, 6*) shows that there are three factors involved in bean height: (1) Determinate versus indeterminate growth; (2) number of internodes (in pole beans this depends largely on environmental conditions); (3) internode length.

Norton (*45*) interprets his results by means of three factors governing height:

A–a. Indeterminate *v.* determinate.
L–l. Tall *v.* short.
T–t. Twining *v.* nontwining.
ALT. Pole beans.
ALt. Runner beans, nontwining pole.
Alt. Shoots from main axis short; some few early, twining shoots.
aLT and *aLt.* Spreading forms with long branches.
alT and *alt.* Erect, bush.

Three-to-one segregations of tall to short have been observed by McRostie (*37*), Tjebbes and Kooiman (*76*), and Doornkaat-Koolman (*4*).

Table 2 gives some bean characters not considered above.

TABLE 2.—*Bean characters*

Contrasted characters	F_2 segregation	Author
Blunt *v.* sharp leaf apex	3:1	Tschermak (*78*).
Broad *v.* narrow leaf	Complex	Emerson (*5*), Wóycicki (*94*).
Long *v.* short internode	do.	Tschermak (*78*), Wóycicki (*94*).
Nonparchmented *v.* parchmented pod	3:1	Emerson (*5*), Tschermak (*78*), Wellensiek (*84*).
Threshable *v.* difficult to thresh	3:1	Tjebbes and Kooiman (*76*).
Yellow *v.* green cotyledon	3:1	Tschermak (*78*).
Yellow *v.* chamois seed	3:1	Nilsson (*43*).
Straight *v.* curved pods	3:1 and 2 modifying factors.	Lamprecht (*26*).
Round *v.* elliptical pods	3:1 and bifactorial	Do.
Normal *v.* unifoliate leaves	3:1	Lamprecht (*35*).
Partially colored seeds	4 or 5 genes	Lamprecht (*31*).
Unlimited *v.* limited growth of axil	3:1	Lamprecht (*34*).
Unbranched *v.* branched inflorescence	3:1	Do.

Disease Resistance

Several strains are known of the organism *Colletotrichum lindemuthianum*, causing bean anthracnose. Burkholder (*2*) and McRostie (*37, 38*) have studied the inheritance of resistance. Where one strain of fungus was concerned, a ratio of 3 resistant to 1 susceptible was obtained; two strains resulted in a 9:7 ratio. Further work is being done on this problem at Cornell University and in the United States Department of Agriculture.

Schreiber (*64*) indicates that there are three independent factors for resistance corresponding to three anthracnose strains.

McRostie (*38*) in crosses involving Robust Pea bean × Flat Marrow observed the F_1 showing a partial dominance of susceptibility. F_2 indicated at least a two-factor difference. Pierce (*52*) and Parker (*47*) have studied the inheritance of resistance to common bean mosaic, using different bean varieties. Parker concluded that since reciprocal crosses gave different results, at least part of the material for resistance was carried in the plant outside the chromosomes. Pierce did not attempt to show a genetic interpretation.

It is interesting to note in connection with the maternal inheritance suggested above that Hoffman (*16*) found that modifications persisted

for six generations after he had treated navy beans with chloral hydrate. These modifications were transmitted only by the cytoplasm of the egg cells and not through the chromatin. It is also of interest to note that Parker (*46*) has found an undoubted case of maternal inheritance of leaf variegation.

Zaumeyer and Wade (*95*) and Pierce (*51*) have indicated that more than one strain of bean mosaic or of legume viruses transmissable to beans are in existence and that bean varieties differ in their reactions to them. Genetic studies of varieties resistant to the viruses are now in progress in the Department.

Rands and Brotherton (*54*) tested the resistance of many varieties and strains of American and foreign beans to several diseases, including at least three strains of the anthracnose organism, bacterial blight, bacterial wilt, and mosaic, and found differential reactions in some cases.

Fromme and Wingard (*8*) made a report on resistance and susceptibility of various bean varieties to rust. There is much material available for genetic and breeding studies in connection with this disease.

McRostic (*38*) made some observations on the inheritance of resistance to dry root rot of beans, caused by *Fusarium martii phaseoli*, but he did not attempt to give a factorial explanation of his results.

Crossing Technique and Interspecific Hybridization

Beans are somewhat difficult to cross, since the curled and brittle style of the flower is easily broken during the process of opening the keel. If the atmosphere is kept near the saturation point for a few days after artificial pollination has been effected, the chances for success are much better than in only a moderately moist atmosphere. The time required to make crosses has prevented genetic studies in *Phaseolus* involving backcrosses.

Many attempts have been made to secure interspecific hybrids within *Phaseolus*, mostly without success except for that involving *P. vulgaris* and *P. multiflorus*. In such hybrids there is usually a great deal of sterility and variability in results, even in the F_1. Mendel (*40*), Doornkaat-Koolman (*4*), Tschermak (*78*), and Tjebbes (*74*) have made studies involving this interspecific cross. At the present time the United States Regional Vegetable Breeding Laboratory, near Charleston, S. C., is testing a variety from Mexico that arose from the cross of *P. vulgaris* with *P. multiflorus*.

Linkage and Cytology

Weinstein (*83*) has shown that *Phaseolus vulgaris* and all other species of *Phaseolus* have 11 pairs of chromosomes.

Tjebbes (*75*) recognizes two linkage groups. Linkage in the *B–A–R–S* group is very close, showing a cross-over value of less than 1 percent between *B* and *S*. *S* is a factor for striping and the other three factors influence the seed-coat color. Genes *C* and *G* are in another group with a cross-over value of about 35 percent.

Several factors give pleitropic effects or the effects are in reality due to more than one factor. However, in such cases it usually requires extensive work to establish the nature of the gene or the closeness of the linkage involved.

Sax (*60, 61, 62, 63*) attempted to analyze quantitative characters by studying their linkage relations to qualitative genes. He demonstrated at least five cases of linkage.

Lima Beans

Only a very limited amount of genetic work has been done with the lima bean (*Phaseolus lunatus* L.). Rhind (*59*) reports genetic studies involving three factors, which he designates as—

R. Rose color seed coat.
P. Intensifies rose to purple seed coat.
S. Speckled seed coat.

Roy Magruder, of the Bureau of Plant Industry, is carrying on genetic studies with *Phaseolus lunatus*.

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IMPROVEMENT IN THE LEAFY CRUCIFEROUS VEGETABLES

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ACCORDING to most botanists, cabbage, cauliflower, broccoli, green-sprouting broccoli, brussels sprouts, kale, collards, and kohlrabi are very closely related, being horticultural forms of the species *Brassica oleracea* L. Kohlrabi is assigned by some botanists to *B. caulorapa* (DC.) Pasq. Wild cabbage (*B. oleracea*), illustrated in figure 1, from which all these forms or varieties are supposed to have arisen, is still found growing wild along coastal regions of Europe and northern Africa. Its use by man as food antedates written history, and it is believed to have been in rather common use for more than 4,000 years.

Figure 1.—A wild cabbage plant.

Just when or where the various forms or varieties of cabbage first appeared or were developed it is difficult to say with any degree of certainty because of the lack of written records. Kale and collards (var. *viridis* L.) are probably the oldest type, and the present wrinkled or ruffled type was mentioned by Theophrastus in 350 B. C. and described and illustrated by Dodonaeus in 1559. Red cabbage or kale was also known to Theophrastus, and Pliny describes heading cabbage (var. *capitata* L.) and includes in his list of types a savoyed or blistered-leaf type which is thought to be the ancestor of our present savoy cabbages. The name savoy indicates that much of the early developmental work occurred in the locality of Savoy in southeastern France. Cauliflower and broccoli (var. *botrytis* L.) are believed to be more recent additions to our types and to have been developed from the green-sprouting broccoli. Kohlrabi (*Brassica oleracea* var. *gongylodes* L., or, if considered a species, *B. caulorapa*) probably was brought north to the low coastal countries of Europe by way of Prague and Vienna. The two most important varieties of today are White Vienna and Purple Vienna. Brussels sprouts (var. *gemmifera* DC.)

were not mentioned by the early writers prior to 1759, but by 1793 this vegetable was an article of international commerce, and its origin is generally ascribed to Belgium.

THE PART PLAYED BY SEEDSMEN IN THE DEVELOPMENT OF CABBAGE

Varieties of vegetables as we speak of them today in our seed catalogs hardly existed before the last of the eighteenth century either in the United States or in Europe. This date corresponds with the rapid rise of seed growing as a business venture in Europe, and no doubt the competition between seedsmen for something new to offer their customers was, then as now, the incentive that led to the rapid introduction of varieties.

The early named varieties were groups of plants with a few common characteristics but many variations. The more observant, careful, and critical growers were always looking for improvements, and when plants were found that seemed superior, these were selected for seed propagation. By continued selection of superior or distinctive types suitable to the particular locality in which the grower lived, many local strains or horticultural varieties—as distinct from botanical varieties—were developed. The local seed seller disposed of any surplus the grower might have, and, as the industry developed, an opportunity was afforded for the general distribution and trial of many varieties over a wide range of conditions. If the variety performed well in its new location, it soon attained major importance. If it was unsuitable in general yet possessed some special merit, it probably was the starting point for a new variety, which was developed as the result of continued selection for the especial point of merit. Thus the early development of all our crops was the work of observant and critical growers who through superior skill in selection and seed growing gradually became the local sources of superior seed. The early seedsmen were merchants, not growers or breeders of seed.

A SINGLE *piece of publicly supported plant breeding saved the cabbage-growing industry in many sections of the country and brought an enormous return on the cost. This was the work begun in Wisconsin in 1910 by L. R. Jones, and continued through the cooperation of J. C. Walker and his associates of the United States Department of Agriculture, to develop varieties resistant to the devastating cabbage yellows or fusarium wilt. As a result, there are now yellows-resistant varieties of all the major types of cabbage demanded by the market. Today other diseases are receiving the attention of breeders, as well as the problem of adaptation of varieties to definite regions and the development of types superior in eating quality and in ability to hold up well in storage.*

The types or varieties of cabbage were developed mainly by the people of the Netherlands, Denmark, Germany, France, and England. When brought to this country by the early settlers, they were not always suited to our climate, which generally was hotter and drier than the climate of the north European countries. The uncertainty of supply and the cost of imported seed forced the isolated grower to attempt to produce seed for himself. Starting with imported seed, he proceeded to select the individual plants that best suited his needs and grow seed from them. If he wanted something earlier maturing, later maturing, with less outer leaves, more rounded head shape, smaller size, more heat-resistance, or what not, he selected toward that goal and in many instances was successful.

The enterprising mail-order seed dealer was largely responsible for the location and introduction to the public of many of these locally developed strains, sometimes with the growers' name affixed but many times with a name selected by the introducer. The high prices paid for these types stimulated seed growers in their effort to find new and superior varieties or strains. Some of the growers soon found they could make more money by growing seed than from the market crop and devoted their energies to seed production. Most of the early cabbage-seed growers were located on Long Island, N. Y., because of the favorable growing conditions there.

At the beginning of the nineteenth century most of the cabbage grown on Long Island belonged to three types: Early York, an early maturing variety with elliptical heads; Flat Dutch, a large midseason variety with flat heads; and Red Dutch, a late, hard, round-headed variety. The Flat Dutch type was more productive and in greater demand on the market than the other two types, and most of the American varieties or strains introduced during the nineteenth century were selections from the Flat Dutch type. An objective of major importance to all growers of cabbage was that every plant should produce a marketable head, and this characteristic is emphasized in the names of some of such varieties as All Head and Surehead. Selections were also made for earlier and later maturing strains of the Flat Dutch type in order to extend the marketing season over a longer period. Some of these selections for difference in maturity resulted in differences in head shape and size and in a rather wide range in type when compared with the parent variety. The early growers were also interested in securing cabbages resistant to disease, and the Houser and Bugner varieties are the results of the efforts of two men along this line. As the seed business became more highly competitive and the growers more critical, the matter of attaining uniformity of type became an object of considerable attention and effort. At the present time there are available very uniform stocks of varieties that cover the entire range of season of maturity and are satisfactory in head size and shape.

A list of the cabbage varieties of known American origin with the year of introduction and other information is given in table 1.

It is also of interest to note which of our present-day important varieties are foreign introductions. In the list of what may be regarded as the nine principal American varieties of cabbage we find Early Jersey Wakefield, Copenhagen Market, Early Winningstadt,

Glory of Enkhuizen, Late Flat Dutch, and Danish Ballhead to be the names of orginal importations, although the present strains of the first and of the last two varieties show a decided improvement in uniformity of type, which may be attributed in part at least to the efforts of American seedsmen. Other varieties of lesser importance that are known to be importations by American seedsmen are Golden Acre, Resistant Detroit, Early York, San Francisco Market, Volga or Early Stonehead, and almost all of the red and savoy varieties.

TABLE 1.—*Cabbage varieties of known American origin*

Variety name	Producer	How produced	Parental variety	Introducer	Year introduced
All Head Early	Mr. Strong, Long Island, N. Y.	Selection	Flat Dutch	W. Atlee Burpee & Co.	1891.
All Seasons (The Vandergaw).	Mr. Vandergaw, Long Island, N. Y.	do	do	James J. H. Gregory.	1886.
Bugner (Bugner Wonderful).	John Bugner, Prairie View, Ill.	Cross and selection.	Unknown	Unknown	About 1890.
Charleston or Large Wakefield.	John M. Brill, Hempstead, N. Y., or Francis Brill, Riverhead, N. Y.	Selection	Jersey Wakefield	F. W. Bolgiano & Co.	About 1866.
Ferry's Hollander	D. M. Ferry & Co.	do	Danish Ballhead	D. M. Ferry & Co.	1900.
Fottler's Early Drumhead or Brunswick Short Stem.	John Fottler, Roxbury, Mass.	do	Frucker Braunschweiger.	A. Schlegel	1866.
Houser	George Houser, Harrisburg, Pa.	do	Stein's Flat Dutch.	Holmes Seed Co.	1897.
Kraut King or Victor Flat Dutch.	Unknown	Cross and selection.	Fottler's Brunswick × Short Stemmed Danish Round.	Unknown	Before 1900.
Newark Early Flat Dutch, Early Flat Dutch, or Early Summer.	Father of Francis Brill	do	French Ox Heart × Large Flat Dutch.	do	Before 1880.
Succession	Abraham Van Seclen, Jamaica, N. Y.	Selection	Early Summer	Peter Henderson & Co.	1888.
Mason	John Mason, Marblehead, Mass.	do	Scotch Drumhead	Unknown	Before 1863.
Stone Mason	John Stone, Marblehead, Mass.	do	Mason	do	Do.
Improved American Savoy.	Unknown	do	Large Savoy	do	Before 1870.
Ferry's Round Dutch.	Ferry-Morse Seed Co.	do	Early Dwarf Dutch.	Ferry-Morse Seed Co.	1933.
Gill's Oregon Ballhead.	Gill Bros. Seed Co.	do	Danish Ballhead	Gill Bros. Seed Co.	1918.
Harris' Ballhead	Joseph Harris & Co	do	do	Joseph Harris & Co.	1932.
Midseason Market	D. M. Ferry Seed Co.	do	Low Late Amager	D. M. Ferry Seed Co.	1921.

BREEDING WORK BY PUBLIC AGENCIES

THE severe losses caused in the cabbage-growing sections of Wisconsin by cabbage "yellows" or fusarium wilt led Jones (*6*),[1] of the Wisconsin Agricultural Experiment Station, to start selection work in 1910 toward the development of yellows-resistant varieties. The work was continued through the cooperation of J. C. Walker, of the United States Department of Agriculture, and his associates (*3, 7, 8, 29, 30,*

[1] Italic numbers in parentheses refer to Literature Cited, p. 298.

31, 32, 33) to the point where we now have yellows-resistant varieties of all the major types. A good example of a yellows-resistant cabbage is illustrated in figure 2. (See the appendix for the list of 10 varieties and years of introduction.) This one piece of publicly supported plant improvement work has saved the cabbage-growing industry in many sections of the country and resulted in an enormous return on the cost.

Workers at the Iowa Agricultural Experiment Station (*14*) have also produced an early yellows-resistant variety of cabbage, Iacope, by selection on disease-infested soil from the Copenhagen Market variety,

Figure 2.—Comparison of yellows-resistant and yellows-susceptible breeding lines of cabbage on heavily infected land. Rows *a* and *c*, resistant progenies; row *b*, susceptible.

and introduced it in 1922. It has since been very largely replaced by earlier and more uniform strains from the Wisconsin work. In 1926 C. E. Myers, of the Pennsylvania station, released a strain of Ballhead called Penn State Ballhead, which was produced by pedigree selection for uniformity and solidity of head and for large yields under Pennsylvania conditions. The work of J. C. Miller, at the Louisiana station, has resulted in the production of a strain called Louisiana Copenhagen, which is earlier, slightly smaller, and shorter-cored and has harder heads under Louisiana conditions than commercial strains of Copenhagen Market, from which it was produced by inbreeding and selection. As a result of the inbreeding, hydridization, and selection work of C. H. Myers and W. I. Fisher at the New York (Cornell) station, nine new varieties or improved strains of cabbage have been introduced.

(See table 4 of the appendix for list and special characters of each.) Several other State experiment stations and the United States Department of Agriculture have cabbage-improvement programs under way from which no introductions have yet been forthcoming (see table 6 of the appendix).

Present Trend in Cabbage Improvement

The major emphasis in cabbage breeding is now upon the development of strains that are resistant to diseases other than yellows, strains that are particularly well adapted to a definite locality, or strains with superior eating or storage quality. There is need for an early-maturing, round-headed, winter-hardy, nonbolting variety of cabbage that can supplant Jersey Wakefield for wintering-over in the South Atlantic coastal region. Our best early round-headed varieties are usually either killed by the cold in this region or produce seedstalks when planted in the fall. Work on this problem is well under way, and it is hoped that within a few years a strain or variety will be available that will combine the hardiness and nonbolting of Jersey or Charleston Wakefield with the more productive and more desirable head characteristics of Golden Acre or Copenhagen Market. Except for sauerkraut manufacture, there is a decided preference for heads of small to medium size, very hard, with mild or sweet flavor and crisp or succulent texture. The development of strains especially adapted to cultural conditions in the large production centers in various sections of the country is another problem on which cabbage breeders are working.

Usual Breeding Method for Biennial Brassicas

In improving cabbage or other Brassicas by selection, commercial seedsmen commonly select several plants possessing the desired characteristics and store them over winter either in cold storage or by burying them in the field under alternate layers of soil and straw or other coarse litter. As soon as the ground can be prepared in the spring, the plants are transplanted to their permanent location. In the case of cabbage, vertical cuts are made on four sides of the head to enable the seedstalk to push through. The mature seed from each plant is saved separately, and the plants that result from it are planted in a separate row the next year. At harvest time only the plants having the desirable characteristics from the most uniformly desirable row (which of course comes from a single head) are selected for storage and seed production the following year. The breeding block and the fields for increasing seed should be at least one-fourth mile distant from any other varieties of Brassicas in order to prevent crossing.

Selfing (applying the pollen of the flower to its own stigma and preventing pollination by other plants) is the most rapid method of securing uniformity in type, but because of the reduction in vigor usually caused by inbreeding the Brassicas, the large proportion of self-sterility present in these plants, and the special equipment and large amount of hand labor required, this method has not come into widespread use by commercial breeders. Various methods of surmounting some of these difficulties are discussed in the section on Developments in Breeding Technique.

American Improvements in Other Brassicas

No plant-improvement work with kohlrabi has been or is being done by any of the American seed growers or the State or Federal research institutions. Cauliflower, likewise, has not been worked with successfully, because of the difficulties attendant upon seed production in this country.

Broccoli seed, however, can be grown successfully in California, and the Ferry-Morse Seed Co. has developed a number of strains that differ in their ability to make marketable heads at different periods through the winter and early spring months. The names November, Christmas, February, March Early, March Late, and April indicate the seasons at which the heads mature most successfully. Green sprouting broccoli, a rather recently revived introduction from Italy, has been much improved in uniformity of type and productiveness by several seed growers.[2] By proper manipulation it can be easily grown as an annual to produce seed the first year.

Long Island Improved, a half-dwarf strain of brussels sprouts selected and improved by early Long Island growers and seedsmen, is the only important variety of this vegetable listed in many American seed catalogs. Very recently the Gill Bros. Seed Co. of Portland, Oreg., has introduced a dark-green strain called Oregon Special, and a medium-green taller strain called Half Moon Bay. The latter probably developed among the growers in the Half Moon Bay section of California.

Improvement work on kale by seedsmen has been limited to fixing the type or selecting more uniform strains. In 1936 the Virginia Truck Experiment Station released a strain of kale and named it V. T. E. S. Scotch. It has blue-green, heavily curled leaves and is more cold-resistant and more uniform than commercial stocks of this Dwarf Blue Curled Scotch type.

Louisiana Sweet is the name of a uniform, shorter petioled, solid green-colored strain of collards introduced in 1934 by the Louisiana Agricultural Experiment Station as the result of several years' inbreeding and selection work in the Georgia collard variety.

Developments in Breeding Technique

As a result of numerous experiments by workers with cabbage and related crops, improvements in technique have been made that greatly facilitate breeding and improvement work. In the work for early-maturing yellows-resistant varieties of cabbage great difficulty was experienced in keeping the plants over winter in storage because of decay and rots that developed during the long storage period. It was discovered that cutting the roots or pulling them loose on one side of the plant and then on the other side at a later date would delay the maturity of the plant until late in the fall. With greenhouse space available, it was possible to transplant the selected plants into large pots, which could then be moved into the greenhouse before freez-

[2] The only consistent difference between broccoli and cauliflower is that broccoli will produce marketable curds during the cold winter weather in the Pacific Coast States, whereas cauliflower requires the warmer weather of the spring season. So the "cauliflower" that easterners get in the winter from the west coast is grown from broccoli seed. "Green sprouting broccoli" does not form a dense 'head" or curd, as is the case with white-heading broccoli or cauliflower, because the floral branches elongate and are not blanched by protecting leaves.

ing weather. When grown at low temperatures until the seedstalk started to elongate, these plants would bloom during early spring and produce seed for sowing in May. This made it possible to treat the usually biennial or perennial cabbage as an annual and greatly speeded up the work. It was also more convenient and easier to do crossing and self-pollination in the greenhouse than in the field. It did not conflict with other field work in the late spring or early summer. Figure 3 illustrates the use of a greenhouse for pollination work.

Figure 3.—Artificial control of cross- and self-pollination of cabbage in the greenhouse. The use of the greenhouse in winter makes it possible to obtain a new generation each year instead of every 2 years.

It was also determined that testing for resistance to yellows could be done as well in the greenhouse under the proper temperature conditions (68° to 77.5° F.) in disease-infested soil as in the field. The plants that proved to be resistant could then be grown to maturity in the greenhouse, and those selected for propagation would produce seed during the winter and early spring without any period in storage, where the plants might be lost through disease or decay.

In breeding for shortness of stem or core, compactness of head, and superior eating quality, it is necessary to remove the head for examination and testing. When cabbages were grown in Louisiana as a fall crop, it was found that the axillary sprouts would develop after the head was cut, and, if the weather was cold enough during December, January, and February, the plants would produce good crops of seed in time to sow for the next fall crop. If the plants were to be

moved into a greenhouse the transplanting was delayed until the lateral sprouts had made a good compact growth.

In some seasons the field-grown plants failed to produce seedstalks and instead produced small heads from the lateral sprouts. Difficulty was sometimes experienced in getting all of the plants to make seedstalks when the material was grown in the greenhouse during the winter. A series of experiments at Cornell University showed that a rest period of approximately 2 months' duration at about 40° F. was required for the subsequent formation of seedstalks. This period could be spent in the fall either in storage or in the greenhouse, and if the temperature was then raised to 70° and maintained there, ripe seed could be produced for sowing in May. Plants that were not given the cold treatment when grown in greenhouses at a temperature of 60° to 70° produced no seedstalks, indicating that a period of low temperature is necessary for the subsequent formation of seedstalks. Increasing the length of day by the use of 5 hours' electric illumination at the end of the daylight period did not cause the appearance of seedstalks in plants grown continuously at the warm temperature (60° to 70°) or hasten their appearance in the cold-treated plants.

In genetic work the use of pure-breeding or homozygous strains is advantageous. Various degrees of self-sterility have been encountered when inbreeding members of the cabbage family to produce such strains. Numerous lines more or less self-fertile have been isolated, but the importance of starting with large numbers of individuals should be emphasized in any program that calls for inbreeding. Experiments to determine the proper time to pollinate cabbage have shown that better seed production results when pollinations are made several days before or several days after the flower first opens. Lines or families that produce practically no seed when pollinated with their own pollen after the flowers open may produce good crops of seed when pollinated from 1 to 5 days before the flower normally opens. Hand-pollination in the bud stage is effected by separating the surrounding sepals with the points of a pair of tweezers and applying the pollen from a mature anther to the exposed stigma. It is not necessary to remove the sepals, and in fact they may be helpful in preventing drying out of the pistils.

It has been well established that not only are there various degrees of self-sterility or self-incompatibility but also there are various degrees of cross-incompatibility among plants of related or unrelated origin. Careful hand pollinations are necessary to determine the exact fertility relations among strains or lines, but the facts when established are useful in working out a breeding program or in the production of hybrid seed on a commercial scale, as pointed out by Pearson (*22*). By planting in alternate rows strains that are self-incompatible but cross-fertile, hybrid seed will result through the action of insects in carrying the pollen from one strain to the other. Bud pollination of a few flower clusters of each strain results in enough seed to perpetuate the strains for later crops. Bees have been found to be very effective agents in the cross transfer of pollen, and by enclosing the individuals or groups of plants under cheesecloth cages the bees may be used in working out the problem of obtaining desirable crosses between different strains or increasing the seed of a number of desirable crosses for preliminary commercial tests (*23*).

When incompatibilities are encountered, it may be possible to continue the improvement work by following a method of alternating selfings with mass increase. The first step is the production by bud pollination of as large progenies as possible of the desirable individuals. Most of the commercially important characters are quantitative in inheritance and large numbers of plants are necessary to produce enough individuals of the desired type. A number of desirable individuals of the same type are selected from the best line or lines and each lot or group is grown in an isolated location, where the plants are open-pollinated. The seed from all the plants of each lot or group are lumped together and sown. Plants of the desired type are selected from the best lots of this planting and bud-pollinated. The seed from each bud-pollinated plant is saved separately and selections for massing are made only from the best lines. In a few years it will be possible to eliminate all but one best line, which, when uniform for the desired characters, may be increased for commercial use.

Propagation of new plants from the axillary buds or sprouts of cabbage has been followed by commercial growers of cabbage when it was desirable to increase the variety or individual as rapidly as possible. Only recently, however, has it been demonstrated (*5*) that vegetative propagation from the head or curd of heading broccoli was possible. The most satisfactory material was from pieces of the curd with scale leaves attached. When placed in a propagating house maintained at 55° F. during the night and with low humidity and plenty of ventilation, these developed roots in 20 days. and in 40 days elongation of the floral axis had taken place.

By transplanting to the field in late spring the shortened stems of plants that had produced a crop of seed in the greenhouse, Miller (*16*) was able to force the development of new heads from lateral buds during the summer and by subsequent cold treatment to produce another crop of seed the following spring. By thus manipulating the environment in which the plants were grown he was able to maintain the cabbage plant as a perennial and yet produce a crop of seed annually.

Pearson (*22*) at the California Experiment Station worked out a rapid and ingenious method for determining the solidity of the cabbage head by determining the apparent specific gravity or density.

CYTOLOGY AND GENETICS OF LEAFY TYPES OF BRASSICA[3]

Cytological investigations of a number of workers have shown that the wild cabbage found along the seacoasts of Europe, various varieties of heading cabbage, kohlrabi, kale, collards, cauliflower, heading broccoli, green sprouting broccoli, and brussels sprouts all have nine pairs of chromosomes ($n=9$). No significant differences have been reported in size or form among the chromosome sets of any of these forms of botanical or horticultural varieties. Hybrids among any of these forms are usually highly fertile, although sterility may sometimes occur, as is pointed out in the section on genetic studies and in the article on root crops (turnips and rutabagas). Botanical varieties of

[3] This section is written primarily for students or others professionally interested in genetics or breeding

Brassica oleracea have been successfully crossed with radish (*Raphanus sativus* L.) (see the article on root crops), and rarely with other species of *Brassica* having different chromosome numbers, the resulting hybrids usually being entirely or highly self-sterile.

The wide diversity of form and function in *Brassica oleracea* would seem to make it an ideal species for genetic analysis, and except for several circumstances, our knowledge might be much more extensive than it is today. Much of the early work cannot be considered dependable because open-pollinated varieties were used. The presence of self-sterility has discouraged many workers from attempting to secure inbred lines with which critical work could be undertaken. Many of the horticultural or botanical varieties require 2 years' time to complete the life cycle and relatively large areas of land. Provision must also be made to prevent cross-pollination by insects. Transference of pollen from anther to pistil must be done by hand or by insects enclosed in the isolation chamber, and extensive use of the backcross is almost prohibitive because of the large amount of hand labor required to get a sufficiently large number of seeds. In spite of these difficulties a number of studies have been made on the inheritance of various characters in the cabbage family. The more important contributions are briefly reviewed below under sectional headings indicating the plant character studied.

In view of the wide range of materials used it is not surprising that the workers report different results with what appear to be the same characters. It is obvious that critical genetic work on the Brassicas has only begun.

Leaf Color

Kristofferson (*12, pt. I*) reports on the inheritance of leaf color in various *Brassica oleracea* botanical and horticultural varieties. He tentatively assumes the interaction of five factors, each with the following effect: *A* produces no color alone, but with *B* produces the dark red violet midrib; *B* causes the light-red midrib; *C* under favorable conditions is able to produce a very faint pink color but with *A* produces the dark-violet midribs of kale; *D* causes the general dark-red color of red cabbage; *E* is concerned with the distribution of the dark red violet color.

The factorial composition of the material with which he worked and its phenotypic appearance with regard to leaf color is given as follows:

Red cabbage, *AbcDe*, dark red violet midrib and blade.
Kale, *Abcde*, green midrib and blade.
Cabbage, *aBCdE*, light-red midrib and green blade.
Brussels sprouts, *aBCdE*, light-red midrib and green blade.
Broccoli, *abCdE*, green midrib and blade.

The evidence presented in support of this hypothesis is far from conclusive, and the author himself in 1927 (*12, pt. II*) concludes: "For a firm establishing of the factorial basis of the total dark red violet color it may be necessary to grow the F_3 generation." He also states in this later paper that the factor *D* "shows any effect only when both factors for violet, *A* and *C*, are present," which is evidently at variance with the scheme proposed in the first paper.

Other workers (*1, 25, 28*) have found a single factor difference between red (purple) and green foliage. Pease (*26*) and Molden-

hawer (*17*) conclude that two complementary factors are concerned in the inheritance of color in a purple kohlrabi × Green Savoy hybrid, for in the F_2 they obtained 9 purples : 7 greens.

C. H. Myers, of Cornell University, has isolated a type designated as magenta that is more nearly red than the so-called red cabbage, which he calls purple. Sun red is also a new foliage color name for a genetic type that shows reddish purple on the stem and midribs and on the edges of leaves on mature plants exposed to sunlight. Genes controlling purple and magenta, magenta and sun color, and sun color and green are reported to be allelomorphs respectively. Crosses between magenta and sun color gave a purple F_1, and 9 purple : 3 sun color : 4 magenta in the F_2. Working with related families, Magruder (*13*) obtained an F_2 of 9 purple : 3 magenta : 3 sun color : 1 green from a cross between a magenta and sun color, indicating the interaction of two independent genes in the production of the purple type studied. There was only a single factor difference between sun color and green and between magenta and green. Kwan (*11*) used different families of the Cornell material and in a cross of purple × sun red the F_2 approximated 15 purple : 1 sun red, suggesting duplicate factors responsible for the purple. The same purple crossed with green gave an F_2 of 9 purple : 3 sun red : 4 green, indicating that this purple was not the same type as that used by Magruder.

In a review of the inheritance of leaf color it is obvious that a standard nomenclature should be used or detailed descriptions given in terms of one of the recognized color dictionaries. Free exchange of genetic color types among investigators would also facilitate a complete analysis of color.

Other Leaf Characteristics

In a cross between wide blade (cabbage) × narrow blade (kohlrabi), Pease (*25*) found the F_1 to approach more nearly the broad type, and in the F_2 the narrow type constituted about one-fourth of the total. Kristofferson (*12*), however, in a cross between broad (cabbage) and narrow (kale) found that the F_1 resembled kale and most of the F_2 plants had more or less intermediate type leaves, but parental types were also obtained.

A type of leaf in which outgrowths of a leafy nature called "asparagodes" occur along the midrib and larger veins at right angles to the plane of the blade was found by Pease (*26*) to be dominant to the normal leaf type and due to a single factor. Detjen (*4*) reports a similar character in his material but believes its expression is due to multiple factors.

The curliness of kale was found to depend on the action of several genes. The F_1 of a cabbage × kale cross is intermediate in curliness, and the F_2 shows continuous variation between the parental types. Malinowski (*14*) assumed three polymeric genes, Allgayer (*1*) four, and Pease (*26*) and Detjen (*4*) an indeterminate number. Kristofferson (*12*), however, reports a red cabbage × kale cross in which the F_2 was relatively uniform and in which neither parental type appeared. Kwan (*11*) crossed wrinkled (savoyed) and smooth-leaved cabbages and concluded that the wrinkled condition is due to the complementary action of two factors. There was no evidence of linkage of either of the factors for wrinkled leaves with either of the complementary factors for purple foliage color.

Contrasting entire with lyrate leaf shape, Pease (*25*) found entire to be due to a single dominant gene.

Petioled type of leaf as contrasted with sessile was found to be due to a single dominant gene by Pease (*25*); but Allgayer (*1*) postulated the action of three genes after his study of a cross between red cabbage and kale. Detjen (*4*) found the F_1 of a cross between winged (sessile) and petiolate to be fully winged, which is the reverse of the condition described by Pease (*25*). He concludes that in his material "clean petiolate head leaves are governed by a recessive factor which may be one of a multiple series." Environment has a marked effect on the expression of this character and makes a study of it very difficult.

Counts of the number of leaves below the mature head showed that in the F_1 the number of leaves was generally that of the parent with the smaller number, but Pearson (*24*) concludes that "according to the evidence, the number of leaves is probably governed by modifying factors."

Height of Plant

Tallness of plants is dominant to dwarfness and is due to a single gene according to Pease (*25*), Malinowski (*14*), and Allgayer (*1*). Kristofferson (*12, pt. II*) found continuous variation in plant height between the parental types in the F_2 and concludes that numerous genes are involved. Detjen (*4*) also concludes that length of stem is dependent upon multiple factors for its expression. Kwan (*11*) obtained plants taller than his tall parent and shorter than the short parent in the F_2 generation, with the F_1 showing marked increase in height over the tallest parent. He says:

> The data suggest that the inheritance of plant height can probably be explained on the assumption that a series of dominant independent cumulative factors favorable for growth are concerned, and that each parent strain carried only part of these favorable factors.

No estimate of the number of factors was made, but the normal distribution of the F_2 population indicated that the factors concerned were of equal value. There was no evidence of linkage between plant height or plant color or foliage surface.

Head Characteristics

Most investigators have found the F_1 from crosses between cabbage and any nonheading *oleracea* (except *gemmifera*) to show a slight heading tendency, and the F_2 to exhibit continuous variation with recovery of both parental types, true heads being in the minority. Malinowski (*14*) and Allgayer (*1*) consider that heading depends on the action of three pairs of genes. Pease (*25*) attributes it to duplicate genes, while Detjen (*4*), working with related headless and heading types of cabbage, found heading to be "fully dominant among related plants, or else the heading factor in headless strains is prevented by one or more factors from clearly manifesting itself."

In crosses between inbred lines Pearson (*24*) concludes that "head shape, in general, is controlled by many factors, of no definite dominance." Crosses between long- and flat-headed strains of Copenhagen Market showed an intermediate shape. "There is some slight evidence that certain head factors are complementary to each other, since one group of crosses produced flatter heads than the parents."

Detjen (*4*) concludes that "head form is not governed by single factors but may depend on a combination of several to many factors."

In crosses between inbred lines Pearson (*24*) found some of the F_1 lines to exceed either parent in weight; in others the F_1 equaled the larger parent; and in crosses between closely related lines no increase in size resulted in the F_1 generation. Detjen (*4*) records several crosses in which plant size of the F_1 showed size equal to or greater than the larger parent.

Crossing brussels sprouts (which have axillary heads but no terminal head) with cabbage (the reverse of brussels sprouts) results in an F_1 that closely resembles the brussels sprouts parent but has a head at the top. In the F_2 there is continuous variation in the tightness of the axillary buds, with a tendency for most of the plants to have loose heads or buds. Kristofferson (*12*) believes the formation of axillary heads is governed by many factors that are independent of factors for the formation of the terminal head.

The formation of axillary shoots is due to a single factor and is recessive to nonformation, according to Allgayer (*1*).

In crosses among inbred strains differing in the relative length of the core, Pearson (*24*) found from his F_1 results that "no dominance is shown in the inheritance of penetration of the core into the head." Hybrids between short- and long-core types have been intermediate in length.

Season of Maturity

By utilizing inbred lines and F_1 hybrids among them, Pearson (*18*) concluded that the season of maturity is—

> dependent in part upon genetic factors, and that hybridization with resulting increase in vigor is not necessarily accompanied by an earlier time of maturity; likewise that environmental differences do not affect all strains in the same way, and that for a definite test, replications together with check rows are very necessary.

Detjen (*4*) says that "heading is found to be governed by a multiple factor for season, which fact explains the many seasonal strains." Rasmusson (*27*) noted an early maturity of the F_1 from crosses among varieties of the same season of maturity. In crosses among early- and late-maturing varieties he notes the F_1 as being only a little later than the earliest parent.

Swollen Stem; Bolting; Corolla Color

The swollen stem or bulb of kohlrabi is incompletely dominant to unswollen stems (as in cabbage) in the F_1, and in the F_2 there is continuous gradation between the parental forms indicating the presence of several genes for bulbing in the kohlrabi. Pease (*26*) presents the clearest data in support of three factors, B_1, B_2, and B_3, of which the first two are major factors and the third a modifying factor. In homozygous condition B_1 and B_2 result in bulb, and when either or both are in heterozygous condition the presence of B_3 converts the stalk into "semibulb" condition. From crosses among related lines of cabbage differing in their stem diameter, Detjen (*4*) concludes that stem diameter is hereditary and dependent on many factors.

Certain varieties are known as "bolters" because when sown in the fall they produce seedstalks instead of heads the following spring. Sutton (*28*) crossed a bolting and a nonbolting strain of cabbage and found the F_1 to be nonbolting and the F_2 to contain approximately 3 nonbolting : 1 bolting. Detjen (*4*), working with strains of cabbage from the Volga variety, found bolting to behave as a monogenic dominant over nonbolting or biennial habit, although he recognizes that bolting is influenced by other genes for time of maturity and heading.

White corolla color was found by Pearson (*19*) and Kakizaki (*10*) to be due to a single gene and dominant to the yellow corolla color.

Self- and Cross-Incompatibility or Sterility

According to Kakizaki (*9*), self- and cross-incompatibility in cabbage is caused by the slow rate of growth of the pollen tubes. In incompatible pollinations the slow growth is due to the presence of a substance that inhibits the growth of pollen tubes through the stylar tissue and in compatible pollinations the normal growth rate of the pollen tubes is due either to the absence of the inhibiting substance or the presence of an accelerating substance able to prevent the inhibiting action. The inhibiting substance is produced most abundantly when the pistil is in full vigor, and its production declines with the decline of the vigor of the pistil. The pseudofertility of bud pollination of incompatible matings is due mainly to insufficient inhibiting action, owing to immaturity of the style, and to the lower time interval for pollen-tube growth, as well as to the shorter distance to be traversed. Kakizaki's results are explained by the hypothesis that two contradictory allelomorphic series of genes are concerned. S_1, S_2, and S_3 constitute the inhibiting series and T_1 and T_2 the accelerating series. The S series is epistatic to the T, but "T in double dose is more active than S in simple dose." In order to explain different degrees of fertility it is assumed that the allelomorphs function in different intensities or that one or more factors of minor value are concerned. When selfed, some self-incompatible plants breed true, while others segregate into 1 self-compatible : 3 self-incompatible. Self-compatible always segregates into 1 self-compatible : 1 self-incompatible. Pearson's (*21*) results "in most respects agree with those of Kakizaki", and Detjen (*4*) likewise agrees that—

> incompatibility in the common cabbage is governed in the main by a series of multiple allelomorphs which result in the manifestation of very distinct types. There are, however, other factors outside of such series that may affect the compatibility of plants such as was observed in the complete reversal of the Zinnia Rosette strain from practically complete self- and cross-incompatibility to practically full self-compatibility. Environmental factors such as temperature also may affect seed setting and temporarily mask the genetical factors.

Resistance to Yellows

Walker (*32*) has clearly demonstrated that resistance to yellows (*Fusarium conglutinans* Wr.) is a monogenic dominant to susceptibility to the disease in most of the yellows-resistant varieties developed by him and his coworkers. Anderson (*2*), one of his associates, has shown that the resistance of Wisconsin Hollander is genetically complex, as it cannot be permanently fixed and is influenced by environmental conditions. When grown at 22° to 24° C. all plants of Wisconsin

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Hollander are susceptible, while resistant types in which the resistance is due to the single dominant factor are fully resistant at these temperatures.

LINKAGE

The results of Pease's work (*25, 26*) indicate the existence of three of the possible nine linkage groups. In the first group are found the genes (or one of a multiple series) for (1) petiolate leaves, (2) one of the genes for head formation, (3) entire leaves, (4) wide leaves, (5) possibly one factor for crinkling of the leaf, (6) bulbing of stem, and (7) red (purple) foliage color. A second group contains (1) a second gene for head formation, (2) a gene for tall plant habit, and (3) probably one of the genes for leaf crinkling.

"Asparagodes" malformation of the leaf thus far has not been linked with either of the above groups.

Malinowski (*14*) and Pease (*25*) report complete correlation between the degree of head formation and curliness in the F_2 of a cabbage$\times$curly kale cross. Malinowski inferred that the heading was due to three pairs of genes, *ABC*, and that curliness is produced by three other pairs of genes, *XYZ*, with complete linkage between *A* and *x*, *B* and *y*, and *C* and *z*.

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IMPROVING THE ROOT VEGETABLES

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Did the ancient civilizations arise in the regions where our common cultivated food plants originated and were naturally abundant? Or did man take food plants with him, so that the early centers of civilization only seem to be the centers of origin of the plants? This must remain an interesting subject of speculation, but few students doubt that civilization was dependent on the natural locations of the plants. At any rate, the regions that are now believed to be the natural centers of origin of the root vegetables (*40, 41*),[1] which were used as food long before recorded history, include practically all of the centers of the oldest civilizations. The present belief is that in the Old World there were six of these, with five of which we are here concerned, and in the New World two major and two minor centers, all of which produced valuable root vegetables:

(1) Central and western China—radish, turnip, taro (dasheen).
(2) India (except northwestern India)—taro.
(3) Middle Asia (Punjab and Kashmir)—turnip, rutabaga, radish, carrot.
(4) Near Asia—turnip (secondary center), beet, carrot.
(5) The Mediterranean—turnip, rutabaga, beet, parsnip, salsify.
(6) Ethiopia—no root vegetables.
(7) Mexico—sweetpotato.
(8) South America (major)—taro, potato.
(8a) Chile—potato.
(8b) Brazil-Paraguay—cassava.

The theory is that the place where a plant exhibits the greatest diversity of subspecies and varieties in its natural state must have been a center of origin of that plant.

The value of the root vegetables is due to the fact that they are biennials, storing food[2] in their roots during the first season to support the second season's growth. Among the cultivated root vegetables, man has been able to select fairly true breeding varieties, which differ from one another chiefly by the shorter or longer time intervals they require to reach maturity. In some regions an ordinarily biennial crop may be changed into an annual, or vice versa, by planting seed early enough so that the plant will bolt, or produce seed the first season, instead of enlarging its root for winter dormancy. In all the biennial crop plants there are numerous varieties reputed to be nonbolters, meaning that they take longer to mature than varieties not so designated. Genetically, the hereditary factors governing time to

[1] Italic numbers in parentheses refer to Literature Cited, p. 322.
[2] The stored food is most frequently in the form of starch and starchlike substances, important elements in the human diet.

maturity in most of our root crops must be numerous, and the terms annual and biennial are not strictly accurate because of the many gradations.

From the beginnings of agriculture almost to the present there has been no conscious effort to improve the root vegetables beyond selecting seed from particular plants whose roots struck the grower's fancy. Within the last century, however, there has been more or less continuous activity in improving plants by crossing diverse types and selecting new combinations of characters. With the development of Mendelism into the science of genetics it became apparent that crossbreeding was essential for rapid plant improvement, and furthermore that an intelligent hybridization technique required a knowledge of the breeding behavior of chosen parents In the case of cross-pollinated species, like the root crops, the breeding behavior or the real genetic make-up of the parents can be determined only by inbreeding to produce lines homozygous or "pure" for their own characteristics. This must be combined with the keeping of pedigree records. With all our root vegetables, however, the inbreeding program is sometimes exceedingly difficult, for two reasons to be discussed later.

IMPROVEMENT OF ROOT CRUCIFERS

THE old method of plant improvement is inadequate for our present needs. The numerous kinds of insects and fungus diseases attacking cruciferous root vegetables (turnip, rutabaga, radish) necessitate the production of new resistant or immune strains by the more recent methods, including inbreeding, crossing, and the use of wild ancestral forms in the search for superior qualities. When established commercial varieties are planted in regions where insects are most numerous or in soils or regions where the fungus diseases are most

THE *old method of plant improvement is inadequate for our present needs. The numerous kinds of insects and fungus diseases attacking such root vegetables as the turnip, rutabaga, and radish necessitate the production of new resistant or immune strains by the more recent methods, including inbreeding, crossing, and the use of wild ancestral forms in the search for superior qualities. In all the cruciferous root vegetables the deliberate attempt to breed for resistance to diseases or to produce special kinds of vegetables has been neglected thus far. But if practically nothing has been done in the way of improvement by modern breeding methods, there has been enough genetic research and working out of adequate techniques to lay the foundations on which to build a practical program.*

damaging, seed can be produced only by plants that are entirely immune or partially resistant to attack. If no natural immunity or resistance is found in commercial stocks, it can usually be found by the introduction of wild ancestral forms of these cultivated vegetables from their original home sites. In all the cruciferous root vegetables the deliberate attempt to breed for resistance to diseases or to produce special kinds of vegetables has been neglected thus far. But if practically nothing has been done in the way of improvement by modern breeding methods, there has been some genetic research and the working out of adequate technique, as will be brought out later. The ground work has been laid on which to build a practical program.

Breeding of Turnip and Rutabaga

The name turnip is commonly applied to vegetables that, in their present cultivated condition, are botanically classified in three separate species of the genus *Brassica*. The point should be stressed, however, that cultivated forms of plants represent complexes of characters that make them quite different from their wild prototypes. This has resulted from many generations of selection for characters, usually Mendelian recessives, which accumulate in combinations not found in nature.

In the United States the name turnip is applied to plants of the species *Brassica rapa* L.,[3] a species wherein all plants examined cytologically have 10 pairs of chromosomes. In Europe the name turnip is frequently applied to the group of plants that we call rutabagas (bagas, or sometimes Swedish turnips), known as *B. napus* var. *sativa rapifera* Hort. by some botanists, and as *B. campestris* var. *napobrassica* DC in Bailey's Standard Cyclopedia of Horticulture. The rutabaga has shown 18 pairs of chromosomes in two cytological examinations by Karpechenko and Frandsen and 19 pairs in one examination by Nagai and Sasaoka (*29*). It is important to know the number of pairs of chromosomes in a species, or at least in the particular stocks used for parents, because crosses between species having unlike numbers of pairs are less easily made and are less regular in breeding and fertility than crosses between those with the same number. A discussion of chromosome numbers in the genus *Brassica* is given by Pearson (*30*).

In general, the chief distinguishing characteristics of the turnip are that the roots are mostly disklike or decidedly flattened, though ranging from spherical to elongated conical; the leaves are hairy, usually not fleshy, and greatly varied in outline; and the plants reach maturity in from 42 to 80 days. The commonly grown varieties show a wide variation in time to maturity, as the following indicates:

	Days
White Milan	42
Snow Ball	43
Purple Top Strap Leaved	46
Purple Top White Globe	55–60
Golden Ball	60–65
Cowhorn	70
Yellow Aberdeen	70–80
White Norfolk	76

[3] Frandsen and Winge (*8*), however, in reporting on the cytology and genetics of the progeny from a cross between the turnip and rutabaga, call the turnip parent *B. campestris* var. *sativa rapifera*, and Vavilov (*41*) calls the turnip *B. campestris* var. *rapifera* Metzg.

The principal turnip varieties reach maturity more quickly than the principal varieties of rutabagas. Since the turnip and the rutabaga will readily cross, however, it is probable that these turnips reaching market size around 65 to 80 days after planting are the results of natural turnip-rutabaga crosses.

The chief characteristics of the rutabaga, or Swedish turnip, as it is sometimes known, are a root that is tankard-shaped or elongated, although sometimes globular; a fleshier and larger leaf than the turnip; leaves not hairy; and a longer period of time (from 85 to 90 days) required for reaching the best pulling stage. Among the most commonly available yellow-fleshed rutabaga varieties on the American market are American Purple Top, Early Neckless, and Bangholm. Two white-fleshed rutabaga varieties are Sweet Russian and White Rock.

Disease Resistance in the Turnip

Although no deliberate attempt has been made to breed disease-resistant varieties of turnips or rutabagas, a new variety of turnip known as The Bruce, that is highly resistant to the slime mold disease called clubroot, has recently been introduced in Great Britain, New Zealand, and Australia. Clubroot attacks many species of the crucifer family, including cabbage, radish, mustard, cauliflower, sweet alyssum, and many others. It is now present in every country where the common cruciferous vegetables are cultivated. The Bruce is supposed to be a natural hybrid between the turnip and the rutabaga, and it first appeared in Scotland about 1820, some 40 years after the time that clubroot first appeared in Great Britain in 1780. The seed of The Bruce was carefully guarded in Aberdeenshire, and as it was disseminated throughout the district it was known to local farmers under different names, until within the last 10 years all agreed on its present name. The variety is still in a highly heterozygous state; that is, it appears in a great range of shapes, colors, firmness of flesh, size of seed, and degrees of resistance to clubroot. Tradition says that the rutabaga parent had a purple top and white flesh and that the turnip parent had a green top and yellow flesh, but these differences are not enough to account for the persistence of a high degree of variability.

Evidently much of the variability is due to the fact that the two parents had different chromosome numbers—10 pairs in the turnip and 18 pairs in the rutabaga—and the present descendants are still segregating for differences in number of chromosomes. From a plant-breeding standpoint it is of interest to note that in tests conducted recently in Scotland (7) the stocks of The Bruce that are less resistant to clubroot proved to be the stocks that have grown on soils less heavily infected with the slime mold.

Many different forms of clubroot exist, and the studies show that different varieties of turnips or rutabagas may be resistant to one or several strains of the slime mold but susceptible to others. Evidently The Bruce combines the largest number of resistance factors, and some strains are therefore nearly immune to this disease.

In addition to the fact that some strains have practical immunity to clubroot, whether grown on limed or unlimed soil, the best strains of the variety also have a higher percentage of dry matter than other turnip varieties included in the same test.

Breeding of the Radish

The radish, *Raphanus sativus* L., is a native of China and India, and its cultivation was practiced in ancient Egyptian and Grecian gardens. Because of its low-food value it has always been more popular as a home-garden vegetable than as a truck crop. It is a good subject for genetic study, since it exhibits a wide range of varietal forms in shape, size, and color of roots, time required from planting to market maturity, and keeping quality. A number of species crosses involving the radish have proved of considerable value to the plant breeder as well as the cytogeneticist. The condition known as self-incompatibility, which means that plants cannot normally be fertilized by their own pollen, is widespread in commercial varieties, but this can be removed by the selection of self-fertile inbred lines.

The leading radish varieties are most frequently classified according to the seasons in which they are grown. Spring varieties, such as French Breakfast, White Tipped, and Scarlet Turnip, are quick-maturing and require from 24 to 30 days' average time to marketing. The leading summer varieties—White Icicle, White Strasburg, and Giant Strasburg—are larger and better keepers and require from about 30 to 42 days to market maturity. The winter varieties, such as Long Black Spanish, Round Black Spanish, White Chinese Winter, and Mammoth White, have the largest roots, require 50 to 60 days to reach market maturity, and keep for several months when well stored.

Our varieties were all developed by crude selection without the aid of artificial cross-breeding to produce special types. A considerable number of genetic analyses have been made with radish, however, and with these as a beginning it is quite likely that plant breeders will take advantage of cross-pollination to produce new forms better adapted for special purposes or localities.

Of great interest from the standpoint of plant breeding is the fact that the radish has been successfully used in generic crosses with the cabbage. According to reliable records, the first successful cross between the radish and the cabbage was made in 1826 by Sageret, a gifted French plant breeder. This wide cross between two genera has subsequently been duplicated by several other investigators, with especially interesting results in the two instances to be reported later.

BREEDING OF THE GARDEN BEET

Although the origin center of the beet, *Beta vulgaris* L., is well known to be western Asia and the Mediterranean region, our commercial varieties have resulted from mass selections, based on the appearance and quality of roots at the end of the first season, to meet western European tastes. The beet flower is largely wind-pollinated, and cross-fertilization can be effected in areas separated a dozen or more miles. The practice of gathering seed for commercial stocks of beets from open-pollinated plants is responsible for the maintenance of self-incompatibility in beet varieties. Recently, however, seedsmen and geneticists are using specially produced inbred lines to obtain improved stocks free from rogues and from self-incompatibility (fig. 1).

The pollination technique in the beet, described later, demands unusual care, because even the protection given by airtight bags will

be undone upon removal to effect controlled cross-pollination unless the breeding plot is removed from possible contamination Self-pollination for inbreeding requires isolation, either geographic or

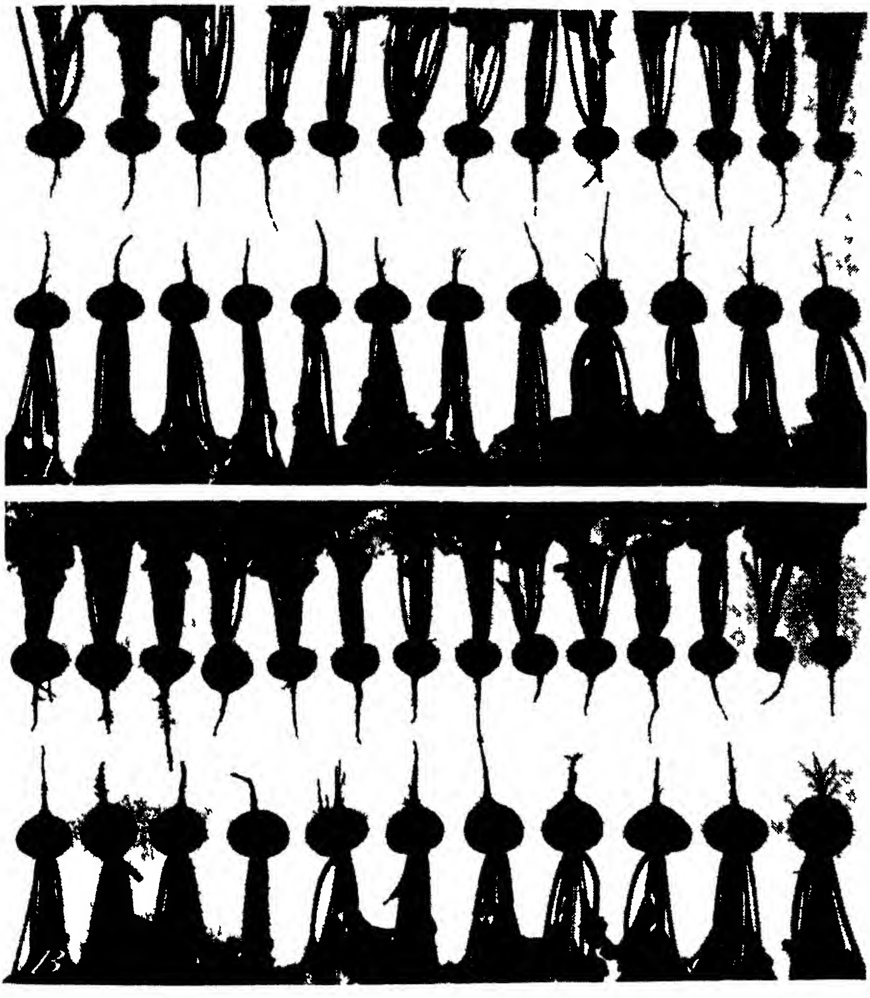

Figure 1 —Effect of inbreeding or line breeding in developing high uniformity and market quality in beets. A, Stock of Ohio Canner developed by selection and line breeding from Detroit Dark Red, B, good average commercial stock of Detroit Dark Red Note superior uniformity in shape of beets in A as compared with those in B

physical, and it is necessary to start with strains that are already self-fertile in some degree

The leading beet varieties differ considerably in length of growing season, and the time to market maturity of the most popular varieties extends from about 57 to 78 days. Beets may be grown so as to be available on our markets all year round by storing the slower-maturing

ones, like Long Smooth Blood, under relatively humid conditions. The leading varieties are all of the red beet type, and they include Asgrow Wonder, Crosby Egyptian, Ohio Canner, Detroit Dark Red, and Long Smooth Blood.

New beet species from Anatolia, recently imported into Germany and examined cytologically by Scheibe (*1*, *33*), have chromosome numbers running in an arithmetical series, with 9, 18, and 27 pairs. A species with 27 pairs, *Beta trigyna* Waldst. and Kit., exhibited a sugar content almost twice as great as that of the best commercial varieties of sugar beets. From the plant breeder's standpoint this information indicates that there are still untried species in the wild origin centers that offer new characters for hybridization and selection. Moreover, the occurrence of chromosome numbers in arithmetical series suggests the operation of chromosome doubling in the evolutionary history of the genus and gives hope of producing new constant-breeding hybrids made to order.

BREEDING OF THE CARROT

Although the home of the carrot, *Daucus carota* L., is western Asia, all of our present varieties represent western European selections, many of which were made by Vilmorin, a French plant breeder and seedsman of the middle nineteenth century. Up to the present, carrot breeding has been almost entirely a matter of crude mass selection, based on the appearance of roots at the end of the first season's growth.

This method has produced a surprisingly good range of varietal types in length and shape of roots, relative thickness of central core, color of roots, and length of time from planting to market maturity. Because of the increasing demand for carrots in the dietary, however, much attention is being given today to the more modern methods of inbreeding for the purification of commercial stocks and for genetic analysis, followed by cross-pollination.

Some notion of the uniformity developed in inbred carrot lines may be gained from the fact that the coefficient of variability in carotene content (carotene is a yellow coloring matter and the source of vitamin A) between 28 roots of a commercial strain of Danvers Half Long was about 33 percent, while the variability between 28 roots of a line inbred for four generations was only about 7 percent.[4]

The leading carrot varieties over the last 20 years have been Chantenay, Danvers Half Long, Oxheart, and Nantes, all of which are medium long, require from 70 to 75 days from planting to marketing condition, and vary from a large core in Chantenay to a minimum of core in Nantes. Although the present trend is to develop narrower cores, there is a limit, because an increasing brittleness of the tops accom-

[4] Influence on carotene content of inbreeding 4 generations (after Emsweller, Burrell, and Borthwick, *6*):

Statistics calculated		Commercial strain	Inbred line
Roots separately analyzed	number	28	8
Mean carotene content	mg. 100 g dry matter	66	56
Range in carotene content	do	32–164	36–80
Standard deviation	do	23.00	4.06
Coefficient of variability	percent	33.6±3.3	7.0±0.6

The average carotene content per line among 18 inbred lines descended from 2 original plants varied from 32 to 63 mg per 100 g of dry matter. One may infer from the above that lines derived from more than 2 original plants would have given a greater spread and therefore offer even better inbred lines with higher carotene content.

panies an increasing narrowness of core. The carrot is the last of the root vegetables to receive the attention of geneticists, owing largely to misconceptions of the difficulties involved. Selected plants were allowed to set seed by open pollination because it was believed that carrots were self-incompatible, and this practice, of course, has largely nullified the effects of the root selection.

For many years carrot growers and seedsmen did not understand that the failure of isolated umbels to set seed was due not to self-incompatibility but to the fact that the stamens of a carrot flower ripen and shed their pollen some hours or days before the pistil is receptive to pollen. Consequently, self-pollination is effective only if the stigmas of the older flowers can be served by pollen from the anthers of younger ones. This service is performed by blowflies introduced into cages in which the entire plant or a major branch is encased; and by using this technique which is described in more detail later, Borthwick and Emsweller (*2*) demonstrated that all carrot varieties tested were entirely self-fertile.

Miller (*28*), in Louisiana, in working with the problem of poor color in carrots grown on certain soils, found that merely selecting the best colored roots on soil that was adversely affecting color produced progenies (whether self-pollinated or open pollinated) having higher percentages of well-colored roots on unfavorable soils than check commercial strains.

Recent studies indicate that hybrid vigor in the carrot acts as it does in corn. When two inbred lines producing roots averaging 12.8 and 24.9 g, respectively, were crossed, the first-generation progeny produced roots that weighed 80.5 g on the average.

Genetic analysis in the carrot has included studies of the inheritance of such characteristics as branched roots, cracked roots, root shape, and root color.

IMPROVEMENT OF OTHER ROOT VEGETABLES

Among the root vegetables taro, parsnip, and salsify are relatively unimportant in the United States, and the number of contrasting characters available for study is so small that no attention has thus far been paid them by breeders or geneticists.

Varieties of Taro

The taro, or dasheen, *Colocasia esculenta* (L.) Schott, seems to have three centers of origin, China, India, and South America, and up to very recent times its cultivation was practically confined to the Hawaiian and other Pacific Islands, where its fleshy root is the staple food of the natives, and also to the Mediterranean region. Recently, however, several introduced varieties of the taro, Trinidad, Ventura, and Sacramento, were thought sufficiently promising to serve as potato substitutes in the Southeastern States (*43*, *44*). As early as the seventeenth century a few varieties were successfully grown in South Carolina as a cheap food source for the plantation hands, but the industry failed to meet competition with importations from the West Indies. The starch of the root is regarded in Hawaii as superior to that of any other root vegetable in the ease with which it is digested and assimilated. Young (*43*) gives many ways in which the taro root may be prepared

as a food, including practically all the ways used with the potato and the sweetpotato.

No breeding or genetic work has been done with taros, and only in Hawaii is there any record of seed production. Moreover, many varieties of taro fail to produce an inflorescence, even in Hawaii. The United States Department of Agriculture has recently begun a project on taro breeding with the object of introducing a large number of species and varieties from Hawaii and elsewhere with a view to investigating their genetics and cytology, and also to provide new varieties with appeal to the growers and consumers of the Southeastern States.

The Parsnip

The parsnip, *Pastinaca sativa* L., is a relatively unimportant root vegetable cultivated in the United States as a market garden crop. Records show that its center of origin was the Mediterranean region and that it was introduced into Virginia in 1609 and Massachusetts in 1629, but thus far there has been no interest in the improvement of varieties or in the analysis of character inheritance. Only one variety of importance, Hollow Crown, is grown in this country, and the lack of varieties with character contrasts is one reason for the failure of geneticists to attempt any character analysis.

The parsnip is an umbelliferous plant in the same family as the carrot, and like the carrot it exhibits the phenomenon of protandry, the pollen being shed long before the stigmas are receptive. The pollination technique of producing pure strains for variety improvement or genetic analysis is therefore identical with that for the carrot.

Salsify

Salsify (*Tragopogon porrifolius* L.) or vegetable-oyster—so called because of a mildly oysterlike flavor—is grown in the United States on a very small scale and is represented mainly by a single variety, Mammoth Sandwich Island. Salsify originated in the Mediterranean area, and its introduction into the United States first occurred about 1806. Practically all the salsify seed produced in this country comes from a narrow strip along the coast of central California. Its limited use, as well as the meager representation of character differences, accounts for the failure of plant breeders or geneticists to take any interest thus far in its improvement.

Salsify is one of the Compositae, belonging to the same family as the sunflower. Its fleshy taproot, which resembles a small parsnip, is handled for curing and storing very much like the dahlia root.

SOME INTERESTING ASPECTS OF ROOT-CROP BREEDING

In spite of the limited amount of practical breeding work with the root vegetables, there are certain aspects of the breeding technique and of the theoretical knowledge attained that are exceptionally interesting from the standpoint of plant breeding in general. An effort will be made here to discuss these aspects as simply as possible for the nontechnical reader. (A technical discussion of root-crop genetics follows later in this article.)

Inbreeding in the root crops is often difficult for two reasons. (1) It brings out recessive factors for small size and lack of vigor; in other words, it is just as likely to make undesirable factors "pure" as desirable ones. Inbred lines frequently are so enfeebled that they cannot live. In carrots, for example, this is so general as to make it necessary to proceed with caution in inbreeding and to inbreed several generations, then outcross to secure enough vigor to go on, then continue inbreeding until the line is as uniform and homozygous or "pure" as desired. With beets, on the other hand, many vigorous upstanding inbred lines have been selected without recourse to outcrossing. (2) Inbreeding may also uncover recessive hereditary factors for self-incompatibility.

How do these factors for self-incompatibility act? In the cruciferous vegetables—including turnip, rutabaga, radish—and probably beets, the rate of pollen-tube growth of all pollen grains containing such a factor is retarded if that factor is also present in the tissues of the style (the stalk of the pistil) through which the pollen tube has to grow before it can reach the ovary; in other words, if the factor is present in both male and female cells (fig. 2). When the rate of pollen-tube growth is retarded the male cell cannot reach the female cell in time to effect fertilization. Self-pollination is thus impossible in plants that lack the normal alternative (allelomorph) of these self-incompatible genes. The difficulty can be overcome, however, by bud pollination; that is, applying pollen to the stigmas of unopened buds. This permits many extra hours of pollen-tube growth before the flower would normally shed its own pollen.

Commercial varieties that contain genes for self-incompatibility cannot be pure or homozygous for this characteristic or they could not reproduce by crossing with other plants of the same variety. They must in some way be cross-compatible with other plants of the variety; that is, in a highly heterozygous condition so far as the genes for self-compatibility are concerned. The best way to remedy this situation is to remove the factors for self-incompatibility that prevent reproduction, by making appropriate crosses to stocks containing the "normal" alternative genes or allelomorphs; or, more simply, all lines that are not self-fertile may be eliminated. The situation is illustrated in figure 2.

The last method has been shown to be entirely feasible even in such characteristically self-incompatible species as cabbage and beets. In these species numerous varieties are available that are completely self-fertile.

All our common root vegetables are biennials, and this somewhat reduces the speed with which breeding operations may be conducted. In each case there are also special impediments to breeding operations, such as self-incompatibility in the cruciferous species, self-incompatibility and wind-pollination in beets, difference in the time of maturity of the male and female organs in carrots, and failure of taro to produce flowers when grown in most regions. These handicaps, however, merely tax the ingenuity of the vegetable breeder and make it necessary for him to develop a special pollination technique for almost every species. To appreciate some of the problems confronting the vegetable breeder, it will be well to review the pollination tech-

nique now most favored for cross-pollination or self-pollination in the root vegetables.

The cruciferous root vegetables—turnips, rutabagas, and radishes—have relatively large flowers, which are insect-pollinated. This makes it necessary, in order to effect controlled pollination, to isolate all flowers from insect contamination by encasing them in cloth or paper bags or in cages made of netting. Crawling insects may be excluded by gluing a cotton lining on the inside of the neck of the bag.

To cross-pollinate, the six anthers from the flower of the female parent must be removed a day before the pollen is shed, thus preventing any chance of self-pollination. The following morning the pollen from the intended male parent, which likewise has been bagged, is applied, either by a camel's-hair brush or by transferring an entire flower that is shedding its pollen, to the stigma of the emasculated flower of the seed parent.

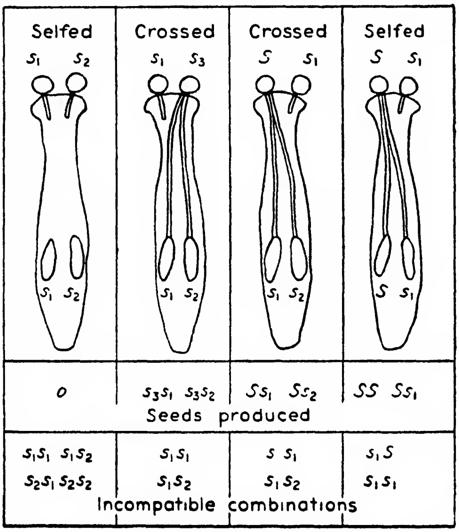

Figure 2.—Diagram showing possible combinations in crosses involving self-incompatibility. *S* represents the normal self-compatible genes, dominant to all the members of the multiple allelomorphic series. s_1, s_2, and s_3 represent self-incompatible genes, recessive multiple allelomorphs of *S*. No plant can have more than two (any two) members of this series.

To self-pollinate, it is necessary, as before, to isolate all flowers from insect contamination. If the plant is self-compatible, it will automatically pollinate itself. If it is self-incompatible, however, it will be necessary to bud-pollinate; that is, to apply pollen from a flower opened this morning to an as yet unopened bud of the same plant. The pollen will thus have extra time in which to reach the ovules. It is even possible that the retarding principle does not become effective until after the pollen of a given flower is shed normally.

The beet is an example of a wind-pollinated species that is also insect-pollinated to some extent. Beet pollen is so small and dust-like that samples of it have been found by airplanes at elevations of 1,000 feet. Consequently when air currents are in motion the removal of a bag in order to effect pollination, even for an instant, may result in contamination of the stigmas with undesired foreign pollen. The best practice is to pollinate in still air; for example, within a greenhouse. The floral organs are so small that emasculation is impracticable. When cross-pollination is desired, an excellent procedure is to make a cross with a male parent that has some easily identified, dominant characteristic. All progeny that result from self-pollination will then show the recessive characteristic and can be discarded in favor of the hybrids, which can be identified by the dominant characteristic; or if it is not completely dominant, they will be intermediate in character.

The technique developed for sugar beets by Brewbaker (*3*) is to isolate the female parent flowers in a hand-made bag 5½ inches by 17 inches made of 30-pound vegetable parchment. When cross-pollination is desired, the danger of uncontrolled pollination may be practically eliminated by not removing the bag at all, and blowing pollen into it with a pollen gun, as described by Jenkins (*13*). As already explained, self-incompatibility in beets and crucifers prevents successful self-pollination unless a normal alternative gene (allelomorph) is present. A strain with such a normal gene might be called a low self-fertile one, and, as indicated in figure 2 (the fourth ovary from the left), a low self-fertile strain may be converted by inbreeding and selection into a high self-fertile strain containing only the dominant normal gene; that is, a strain homozygous for self-fertility.

As a result of inbreeding experiments with sugar beets, Brewbaker (*3*) says: "The characters of high and low self-fertility appear to be heritable, and by selection and continued self-pollination highly self-fertile lines would be obtained." It should be said that no genetic analysis of the inheritance of what is called self-sterility in beets has been made, but it is assumed to be of the same nature as that outlined in figure 2, which in general illustrates the interaction of genes for self-incompatibility in the cases thus far studied, tobacco and cabbage.

In carrots no self-incompatibility is encountered, despite previous beliefs (*2*). Self-fertility is complete provided one overcomes the barrier of protandry, which can be easily done by using the fly-pollination technique of Jones and Emsweller as applied to carrots by Borthwick and Emsweller (*2*), for either cross-pollination or self-pollination.

Since carrot flowers are as small and difficult to emasculate as beet flowers, cross-pollination is effected most readily by bagging single umbels in muslin or cheesecloth bags, waiting several days after the first flowers have come into full bloom, then introducing an umbel of the male parent with cut stem in a jar of water, along with a supply of freshly hatched clean blowflies, which will effectively transfer the pollen to the female umbels. In such cases self-pollination is impossible on a single umbel because of the existence of protandry. Self-pollination is readily performed by caging an entire plant in a muslin or cheesecloth bag, then periodically introducing clean freshly hatched flies. By caging the entire plant the flies are enabled to pollinate the older flowers with their own kind of pollen from the younger flowers.

The technique of pollination in taros is very simple. The taro flower is in the form of a spadix or fleshy axis enclosed by a modified leaf or spathe, as in the jack-in-the-pulpit or the calla. Each spadix contains staminate florets on its upper end and pistillate florets on its lower end. All that is required is to remove the spathe and enclose the spadix in a glassine or other transparent bag to exclude insects, and self- or cross-pollinate the female florets as desired with a camel's-hair brush. This is sometimes impossible on a single spadix because in some species of taro the stigmas are past receptivity by the time pollen is ready. (This is known as protogyny, the opposite of protandry.) As a precaution against self-pollination when crossing is desired, it is

advisable to remove the male end of the spadix. The real difficulty with taro, however, is that most varieties will not produce an inflorescence even where they are extensively cultivated, as in Hawaii.

Hybridization between species or genera of the root vegetables has produced at least three artificial hybrids with all of the chromosomes doubled. Plants with doubled chromosome numbers of this kind are known as amphidiploids, and they are usually hybrids between remotely related parents. It would seem that on account of the remote relationship, the chromosomes of the parents are so dissimilar as to be unable to mate or pair properly. The cell-division mechanism is consequently so fundamentally disturbed as to produce a doubling of the number of chromosomes in the sex cells. The first-generation hybrid is likely to be either entirely sterile or almost so, but the doubling of the chromosome number provides all unmated chromosomes with mates for pairing, so that in future generations sex cell division can proceed in the regular manner. The result may be a true-breeding amphidiploid. In figure 3 all visibly unpaired chromosomes of the F_1 or first hybrid generation can be seen to be doubled in the amphidiploid hybrid. Frequently, however, the chromosome doubling takes place in the cells of the plant body instead of in the sex cells.[5]

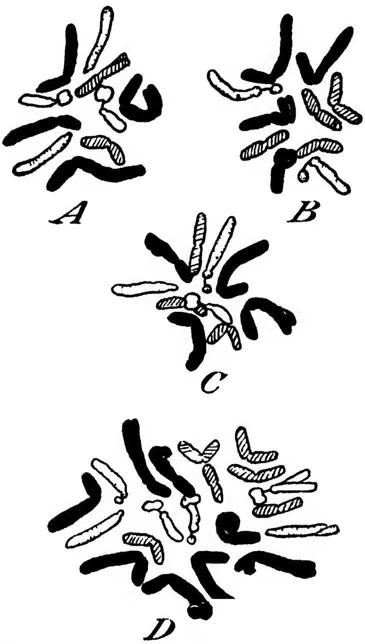

Figure 3.—Somatic (diploid) chromosome sets of two parent species of hawks-beard: *A*, *Crepis rubra*; *B*, *C. foetida*; *C*, their F_1 hybrid; *D*, their amphidiploid hybrid. Chromosome doubling in some F_1 sex cells, followed by a union of two of them, has produced a complete diploid set, qualitatively as well as quantitatively, from both parents. × about 1,800.

It was only in 1925 that the first amphidiploid hybrid obtained under experimental conditions was recognized and described (*4*). Since then an almost bewildering number of such hybrids have been described. Many of them, because of the wide separation of their two parents, are practically true-breeding and might truly be called new genera or new species and given new names (*42*). In other cases, however, the parent species were so closely related to begin with that many of the chromosomes were able to pair, and the subsequent chromosome doubling therefore only resulted in a more complex hybrid, but not a true-breeding one or one that could be expected to produce stable derivatives (*31*, *32*).

Many plant genera contain species whose sex cell chromosome numbers occur either exclusively or mostly in multiples of some common number. In wheat (*Triticum*), for example, some species

[5] That is, amphidiploids may be formed in two ways—in the gametophyte or sexual generation, and in the sporophyte or asexual generation.

have 7 chromosomes, others 14, and still others 21, in an arithmetical series. Other examples of genera in which this occurs, with the sex cell chromosome numbers, are:

Beta (beet)	9, 18, 27
Campanula	17, 34, 51, 8, 16, 10, 13
Chrysanthemum	9, 18, 27, 36, 45
Papaver (poppy)	7, 14, 21, 28, 11, 22
Rosa	7, 14, 21, 28

The occurrence of arithmetical series among the chromosome numbers of many genera prompted Winge in 1917 to offer the hypothesis that such chromosome numbers arose as a consequence of chromosome doubling following species crosses. At that time he knew of no experimental verification of his hypothesis, but now there are scores of artificially produced amphidiploids, as well as evidence of amphidiploid hybrids in the wild, and correlated analyses of characters and chromosome numbers for their parent species. Two species known to be natural hybrids are successfully growing in the wild—one a pentstemon, in the foothills of California, and the other a grass, in the harbors and on the beaches of the English Channel. The artificially produced constant breeding amphidiploids in the Cruciferae, with the number of pairs of chromosomes, are:

(1) Radish, *Raphanus sativus*, 9 pairs, × cabbage, *Brassica oleracea* L., 9 pairs, produced "*Raphanobrassica*", 18 pairs.
(2) Radish, *R. sativus*, 9 pairs, × Chinese cabbage, *B. chinensis* L., 10 pairs, produced "*Brassicoraphanus*", 19 pairs.
(3) Turnip, *B. campestris* L., 10 pairs, × rutabaga, *B. napus*, 18 pairs, produced "*Brassica napocampestris*", 28 pairs.

Although none of these constant breeding hybrids has commercial possibilities at present, *Brassica napocampestris*, combining features of the turnip and the rutabaga, may easily have value with further selection, and the others can be used as parents for further crosses to provide selection material for commercial stocks.

The fact that the chromosome numbers in *Beta*, from which our garden and sugar beets come, occur in an arithmetical series, 9, 18, 27, suggests that species formation in this genus was influenced to some extent by chromosome doubling following crosses between species.

GENETICS OF THE ROOT VEGETABLES [6]

Turnip and Rutabaga

According to Kajanus, turnip more commonly contains hereditary factors for self-incompatibility than rutabaga. This is expected if among the larger number of chromosomes of the rutabaga the chromosome containing the locus S versus s_1, s_2, etc. (see fig. 2), had been duplicated; hence segregations for compatibility versus incompatibility will show at least a tetraploid rather than a diploid ratio; for example, an expectation of 35:1 instead of 3:1. The production of self-fertile inbred lines in turnips will, therefore, be more difficult than in rutabagas.

Kajanus (*15, 16, 17, 18, 19*) has made the greatest number of genetic analyses in both these species, the main results of which are shown

[6] This section is written primarily for students or others professionally interested in breeding or genetics.

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in tables 1 and 2. Among other geneticists who have worked with these vegetables are Hallqvist (*11*, *12*), Malinowski (*25*, *26*), and Sylven (*34*). Kajanus studied the progeny of hybrids between these two species, and Frandsen and Winge (*8*) produced an F_1 hybrid between the turnip and the rutabaga that later doubled its chromosome number. The ensuing amphidiploid stock of plants had the potentialities of a constant new species, combining features from both parents, but most of them came from the rutabaga, because it contributed most of the chromosomes.

TABLE 1.—*Genetic analyses of character inheritance in turnip*

Symbols	Phenotypes		
	Color of bark	Color of flesh	Color of flower
PVM	Red	White	Yellow
PVm	do	Yellow	Orange
PvM	do	White	Yellow
Pvm	do	Yellow	Orange
pVM	Green	White	Yellow
pVm	do	Yellow	Orange
pvM	Yellow	White	Yellow
pvm	do	Yellow	Orange

M v. m, white *v.* yellow flesh color, also yellow *v.* orange flower color
P v. p (anthocyanin), red *v.* cream-yellow upper root bark color.
V v. v (chlorophyll), green *v.* cream-yellow upper root bark color
P is epistatic to *V*, thus producing the phenotypic combinations shown above.
Mendelian ratios obtained (Kajanus):

Bark color—12 red : 3 green : 1 yellow.
Flesh color—3 white : 1 yellow.
Flower color—3 yellow : 1 orange.
Root shape—multiple factor inheritance
Root surface—3 cracked : 1 smooth.

The heterozygotes of these genes exhibit an intermediate intensity of expression; consequently the classification of any hybrid population may be more complex than is indicated.

TABLE 2.—*Genetic analyses of character inheritance in rutabagas*

Symbols	Phenotypes			
	Color of bark	Color of flesh	Shape of leaf	Color of flower
$P_1P_2M_1M_2E_1E_2AB$	Deep red	White	Pinnatifid	Yellow
$p_1P_2M_1M_2E_1e_2Ab$	do	do	do	Orange
$P_1P_2M_1m_2e_1e_2aB$	do	do	Entire	Pale yellow
$P_1P_2m_1M_2E_1E_2ab$	do	do	Pinnatifid	Pale orange
$P_1p_2M_1M_2e_1e_2AB$	Pale red	do	Entire	Yellow
$P_1p_2M_1m_2e_1e_2Ab$	do	do	do	Orange
$p_1p_2M_1M_2E_1e_2aB$	Green	do	Pinnatifid	Pale yellow
$p_1p_2m_1m_2e_1e_2ab$	do	Yellow	Entire	Pale orange

A v. a, orange *v.* pale orange flowers.
B v. b, yellow *v.* pale yellow flowers.
P_1 *v.* p_1, pale violet red *v.* green.
P_2 *v.* p_2, deep violet red *v.* green.
M_1M_2 *v.* m_1m_2, yellow *v.* white flesh color.
E_1E_2 *v.* e_1e_2, pinnatifid *v.* entire leaf outline.
P_2 is epistatic over P_1, giving the phenotypes shown above.

Mendelian ratios obtained:

Bark color—12 deep red : 3 pale red : 1 green (Kajanus and Hallqvist).
Flesh color—15 white : 1 yellow (Hallqvist).
Leaf shape—15 pinnatifid : 1 entire (Hallqvist).
Life cycle—Biennial *v.* annual, multiple factors (Malinowski).
Flower color—9 yellow : 3 orange : 3 pale yellow : 1 pale orange (Sylven).

The duplicate nature of factorial relations here is an additional reason for the suggestion that the genes concerned are included in the extra set of eight chromosomes by which the rutabaga is distinguished from the turnip. For example, the two 15:1 segregations for flesh color and leaf shape indicate duplicate dominant genes for the dominant allelomorphs in each case. Malinowski, who analyzed the cross biennial × annual, obtained an observed ratio of 349 biennials to 57 annuals, which gives a significant deviation from any assumed Mendelian ratio.

Turnip × Rutabaga Crosses

From 1912 to 1917 Kajanus reported studies from a number of crosses between the two species, turnip, *Brassica rapa* (10 pairs of chromosomes), and rutabaga, *B. napus* (18 pairs of chromosomes), with results that have been summarized by Matsuura (*27*). The work was done before the acceptance by geneticists of cytological aid in investigating crosses between parents with differing chromosome numbers. The studies summarized by Matsuura would have been more valuable had the investigators considered this feature of the problem. Most of the analyses made, however, deal only with simply inherited leaf characters that segregate in the F_2 generation with 1:2:1 monohybrid ratios, as, 1 pubescent : 2 intermediate : 1 smooth; or 1 bloom : 2 intermediate : 1 nonbloom.

The Amphidiploid Hybrid "Napocampestris"

In 1932 Frandsen and Winge (*8*) reported the production under experimental control of a hybrid between the turnip, *Brassica campestris* var. *sativa rapifera* (10 pairs of chromosomes) and the rutabaga, *B. napus* var. *sativa rapifera* (18 pairs of chromosomes). It is unfortunate that an unnecessary confusion should be introduced by calling the turnip *B. campestris* here and *B. rapa* at other times, but the authors' names have been used. As expected, plants of the first filial generation were, as a rule, quite sterile compared with the parent plants. One of the F_1 plants, however, proved to be almost as fertile as the parents. A cytological examination of the root tips of several F_1 plants showed the expected chromosome number of 28 (10 plus 18), where half the chromosomes from rutabaga were added to half the number from the turnip parent. Consequently it is believed that all the F_1 plants, with the exception of the one that was highly fertile, possessed 28 somatic chromosomes. The highly fertile plant is believed to have doubled its chromosomes from 28 to 56 immediately following fertilization, as in *Nicotiana digluta* (*4*), because in the progeny of this plant 21 plants that were examined cytologically were highly uniform both as to outward appearance and as to the chromosome number of 56.

The progeny of all 28-chromosome F_1 plants exhibited a more or less high degree of sterility, because at the time of formation of sex cells the 18 chromosomes from the rutabaga parent had only 10 chromosomes from the turnip parent with which to mate, leaving 8 chromosomes to be distributed to the sex cells at random. Consequently, when these plants were self-pollinated, all sorts of fertilizations with odd chromosome numbers were effected, many of which proved to be nonviable, hence the high degree of sterility. Sterility of this kind is called "generational" sterility, to distinguish it from incompatibility, already considered. In the progeny of the 56-chromosome fertile plant, however, the distribution of chromosomes to the new sex cells was as regular as though the plant had 28 pairs of chromosomes, the members of each pair separating from each other at germ cell formation with the regularity of true-breeding natural species.

An idea of the uniformity of this fairly true-breeding new hybrid may be gained by comparing its F_2 progeny with the parents and the F_1 generation.

Rutabaga: Oval root, red-violet bark, yellow flesh.

Turnip: Elongated root, green bark, yellow flesh.

F_1 (a): The seed of two plants gave half-long roots, red-violet bark, and yellow flesh in the progeny.

F_1 (b): The seed of one plant gave half-long roots, one-half red-violet and one-half green bark, and yellow flesh.

F_2 generation is shown in table 3.

TABLE 3.—*Distribution of root shapes of turnip-rutabaga hybrids*

Nature of hybrid	Globe	Oval	Half long	Long conical	Bark color
	Percent	*Percent*	*Percent*	*Percent*	
Diploid	17	18	53	12	Various
Amphidiploid			84	16	Green

In outward appearance as well as in chromosome content most of the progeny, diploid or amphidiploid, resembled the rutabaga parent which contributed eight more chromosomes than the turnip. This may be compared to the observation that in The Bruce turnip most of the characters usually favor the presumed rutabaga parent. From the foregoing discussion of Kajanus' analysis of inheritance of root color in turnips and rutabagas it is seen that green bark is hypostatic to red bark, which indicates that the rutabaga parent of Frandsen's amphidiploid hybrid must have been heterozygous for the red bark factor, and therefore of the genotype *PpVV*.

GENETICS OF THE RADISH

An outline of the chief genetic analyses in the radish, *Raphanus sativus*, together with the names of the investigators reporting them, is given in table 4. The list is compiled chiefly from the work of Frost (*9*), Uphof (*39*), and to a lesser extent Malinowski (*25*) and Karpechenko (*21*, *22*). The character contrasts include all organs of the plant, and the segregations reported show that a fairly simple factorial situation usually exists.

Some question arises regarding the interpretation of results from the cross red-striped *v.* white (made from crossing the variety Triumph with either Early White or Icicle). In F_1 red-striped was completely dominant to white, but in F_2 instead of 3 red-striped:1 white, Uphof obtained 1 red-striped:1 white. No cause of the supposed disturbed ratio was learned, but Uphof suggested the action of a gamete lethal, although this ratio might actually be a 9:7 interaction, in which two recessive whites are involved. Frost's crosses in some cases showed a pronounced hybrid vigor in F_1, a phenomenon most frequent in open-pollinated species maintained in a highly heterozygous state.

TABLE 4.—*Character inheritance in Raphanus sativus*

P_1 characters	F_1	F_2	Investigator
Root			
Yellow *v.* white	Yellow	3 yellow 1 white	Uphof, Malinowski
Red *v.* white	Purple	1 red 2 purple 1 white	Uphof
Purple *v.* red	do	3 purple 1 red	Frost
Red primary cortex *v.* white	Red	15 red 1 white	Uphof
Red striped *v.* white	Red striped	1 red striped 1 white	Do
Long *v.* globe	Intermediate	1 long 2 intermediate 1 globe	Do
Corky *v.* smooth	Corky	3 corky 1 smooth	Do
Long leaf *v.* short	Intermediate	1 long 2 intermediate 1 short	Do
Early flowering *v.* late	Early.. .	3 early.1 late.....	Frost
Inflorescence:			
White *v.* yellow	White	3 white 1 yellow	Karpechenko
Woody capsule *v.* papery	Woody	Complex inheritance	Frost

Linkage —Purple *v.* red and early *v.* late are on the same chromosome

Species Crosses in the Radish

Crosses are easily made between the wild radish, *Raphanus raphanistrum* L., yellow flowered, and the cultivated radish, *R. sativus*, red, purple, or white flowered. Both species have nine pairs of chromosomes, and the cross appears to segregate regularly both as to chromosome distribution and Mendelian factors. F_1 interspecific hybrids usually have violet flower color, and, according to Trouard-Riolle (*36*, *37*), the starchy root of the wild radish is dominant over the sugary root of the cultivated radish. Frost found indications of a linkage between the locus for purple-red root pigment and that for earliness *v.* lateness of flowering, with a cross-over of 4.78 percent. Frost also established the presence of self-incompatibility in the radish, but made no analysis of its genetics.

Karpechenko's "Raphanobrassica"

Karpechenko (*21*) obtained a first-generation hybrid between the radish ($2n=18$) and cabbage ($2n=18$) which was highly sterile as a result of disparity in chromosome content and structure, although not in chromosome number, between the two parent species. In consequence of the cell-division disturbances, some of the functioning sex cells had double the expected number of chromosomes. The chance conjugation of two such unreduced sex cells resulted in the production of a plant having the combined diploid number of chromosomes of the two parents, known as an amphidiploid hybrid. Karpechenko's amphidiploid hybrid was in some respects like the

amphidiploid hybrid that Frandsen obtained in the turnip-rutabaga cross already described. There is one important difference, however, between Karpechenko's radish-cabbage amphidiploid and Frandsen's turnip-rutabaga amphidiploid. Frandsen's hybrid presumably resulted from a suspended cell division following the union of the turnip sperm with the rutabaga egg, whereas Karpechenko's hybrid resulted from the chance meeting of two unreduced sex cells in the ovary of a first-generation hybrid. Thus we have illustrations of the two ways in which amphidiploids can be produced; (1) where the doubling occurs in the asexual or sporophyte generation, and (2) where the doubling occurs in the sexual or gametophyte generation.

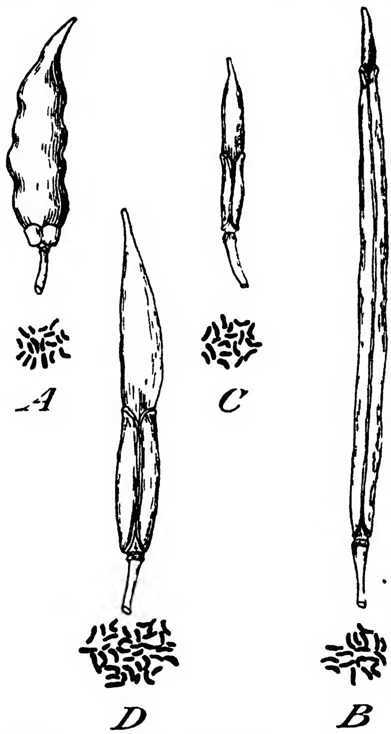

Figure 4.—Diagrammatic representation of the relative capsule shapes and sizes, as well as chromosome numbers, in (*A*) *Raphanus sativus*, (*B*) *Brassica oleracea*, (*C*) their F_1 hybrid, and (*D*) their amphidiploid hybrid. Redrawn from Karpechenko, but the relative chromosome sizes were somewhat enlarged in the copying.

Figure 4 presents a diagram of the types of seed capsules characteristic of the parents and hybrids occurring in the production of Karpechenko's amphidiploid, which he called *Raphanobrassica*. The hybrid plants were clearly intermediate between the two parents in the structure of capsules, as will be seen from figure 4, but also in possessing as many kinds of chromosomes from one parent as the other—radish, *Raphanus satirus* ($2n=18$); cabbage, *Brassica oleracea* var. *capitata* ($2n=18$); *Raphanobrassica* ($2n=36$).

No effort has been made to utilize *Raphanobrassica* to improve either the radish or the cabbage, and Karpechenko (*22*) states that it will not cross back to either of its parents. It will cross readily, however, with a large number of other cruciferous species, including turnips and rutabagas, which in turn will not cross with either radish or cabbage. Karpechenko attempted to produce still other amphidiploids with an even higher chromosome number by adding the chromosomes of turnip, rutabaga, etc., to those of *Raphanobrassica*. The first-generation hybrids have succeeded, but thus far the chromosome doubling to stabilize sex cell formation has not occurred.

From the plant-breeding standpoint the chief value of these studies is the demonstration of the principle that if a cross cannot be made directly between species *A* and *B* because of their wide evolutionary separation, then the gap may be bridged by first forming a hybrid between *A* and *C*, with which *B* will later successfully cross.

Terasawa's "Brassico-raphanus"

In 1932 Terasawa (*35*) reported the appearance of an amphidiploid hybrid called *Brassico-raphanus* with $2n=38$ chromosomes, which bred approximately true in the F_4 generation from the cross pakchoi (*Brassica chinensis*, $2n=20$) × radish (*Raphanus sativus*, $2n=18$). He explained the tardy appearance of this amphidiploid in F_4 instead of F_2 as resulting from insect pollination of F_2 plants, which somehow induced nonreduction of chromosomes in sex cells. Consequently, the origin of *Brassico-raphanus* from unreduced gametes was in the main similar to that of *Raphanobrassica*. The phenotypes of the two parents and their intermediate hybrid are shown in table 5.

TABLE 5.—*Comparative morphology of Brassica chinensis, Raphanus sativus, and their amphidiploid*

Species	Leaf margins	Roots	Flower color	Calyx	Fruit structure
Brassica chinensis	Entire	Slender	Yellow	Open	2 locules.
Raphanus sativus	Lobed	Fleshy	Purple	Closed	Not dehiscent.
Brassico-raphanus	Intermediate	Quite fleshy	White with purple veins	Intermediate	Upper half not dehiscent, lower 2 locules.

GENETICS OF THE BEET

Our knowledge concerning the genetics of *Beta* is obtained chiefly from the investigations of Kajanus (*14, 16, 20*) and Keller (*23*). Some years ago Kajanus, also Lindhard and Iversen (*24*), investigated the inheritance of root color in this biennial root crop, and all believed that the postulation of two pairs of factors was sufficient to account for color inheritance. Certain discrepancies in Kajanus' segregation, which he ascribed to faulty pollination technique, were observed also by Lindhard and Iversen, who interpreted them as caused by about 37-percent linkage between the two postulated loci. More recently, however, Keller, with greater care against the contamination of wind-pollination, investigated the genetics of root color. Instead of only the two pairs of factors assumed by Kajanus et al., giving 4 segregating phenotypes in F_2, he finds that each of the two loci carries a series of three multiple allelomorphs.

The genes postulated by Keller in the order of their dominance are:

Locus 1. R=red hypocotyl, R^t=red top white hypocotyl, r=yellow hypocotyl.
Locus 2. Y=yellow root, Y^r=green top yellow root, y=white root.

From two different F_2 populations the following series of nine phenotypes was obtained from combinations of these six genes:

Root phenotypes in garden-beet crosses

Phenotypes	*Symbols*
Red hypocotyl, white root	Ry
Red hyopcotyl, red root	RY
Pale red hypocotyl, pale red root	$RY\pm$
Striped red beet	R^tY^r
Green top, red root	RY^r
Red top, white root	R^ty
Yellow hypocotyl, white root	ry
Green top, yellow root	rY^r
Yellow beet	rY

Moreover, instead of a loose linkage of 37 percent, he calculated an average linkage of 7.3 percent for four crosses made in the coupling phase and a linkage of 8.8 percent for a single cross made in the repulsion phase. Different members of the multiple allelomorph series were used in the two types of crosses, as shown in table 6.

TABLE 6.—*Linkage values derived from beet crosses in the coupling and repulsion phases*

Crosses	Parental combinations		Recombinations		Total
	R^tY^r	ry	R^ty	rY^r	
Coupling phase crosses. Recombination percentage=7.3:					
$\frac{ry}{ry}\times\frac{R^tY^r}{ry}$	97	114	14	5	230
$\frac{R^tY^r}{ry}\times\frac{ry}{ry}$	145	137	7	12	301
$\frac{ry}{ry}\times\frac{R^tY^r}{ry}$	89	162	9	8	268
$\frac{R^tY^r}{ry}\times\frac{ry}{ry}$	133	109	12	11	265
Total	464	522	42	36	1,064
	Ry	rY^r	RY^r	ry	
Repulsion phase cross. Recombination percentage=8.8:					
$\frac{Ry}{rY^r}\times\frac{ry}{ry}$	315	307	23	37	682

Kajanus also investigated the genetics of leaf color, but found the ratios less satisfactory than for root color. In the red-fleshed beets the distribution of anthocyanin is sometimes general throughout the stems and leaves and sometimes confined to the stems, petioles, and larger veins, the rest of the leaf being green. Crosses between red-containing phenotypes and entirely green-leafed ones gave conflicting results. Sometimes green appeared to be dominant to red and at other times it was clearly recessive. He interpreted this paradox to indicate the presence of a dominant inhibitor for red leaves in some genotypes which is absent in others.

Finally, for root shape, Kajanus postulated four pairs of genes:

L v. l, long root *v.* short.
O v. o, inhibitor of *L v.* noninhibitor.
A v. a, sharp *v.* blunt forms.
B v. b, inhibitor of *A v.* noninhibitor.

It has already been noted that the root crops carry several genes for self-incompatibility, and *Beta vulgaris* is no exception. Although no attempt has been made to study the inheritance of self-incompatibility in *Beta*, it is easy to keep these genes out of the populations by selecting self-fertile inbred lines. The Division of Sugar Plant Investigations of the Bureau of Plant Industry has selected several completely self-fertile strains of sugar beets, and Roy Magruder, of the Division of Fruit and Vegetable Crops and Diseases, has several promising inbred lines of garden beets.

Dudok van Heel (*5*) with sugar beets and Bateson (*10*) with sugar, garden, and stock beets, have investigated the inheritance of bolting. Both investigators thought inbreeding in beets was impossible because of self-incompatibility, and thus made their selections from open-pollinated mother plants. Despite the poor pollen control, both were able in a short time to select lines that were practically or entirely nonbolters under any conditions. Bateson rapidly eliminated bolters by forcing under glass. Dudok crossed high-bolting and low-bolting strains and found evidence in F_1 that low bolting or nonbolting was dominant, but he attempted no further analysis.

In view of the fact that in radishes Frost found high bolting to be completely dominant to low bolting in the ratio of 3 : 1 in F_2, and that in rutabagas Malinowski found low bolting partially dominant in F_1 and F_2 with indication of multiple factors, it is regrettable that more complete information is not available for beets. It is probable that many genetic factors are in operation, from the fact that a wide range exists between beet varieties in length of time to market maturity.

Genetics of the Carrot

The project of producing inbred lines in carrots as the initial step in genetic analysis was begun at Davis, Calif., for the purpose of general genetic analysis, variety improvement, and increase of carotene content. The attempt to increase carotene content in the carrot is important, because it is a rich source of vitamin A, so necessary in the correction and prevention of certain nutritional disorders. Betacarotene and vitamin A appear to produce identical physiological effects. The general genetic analysis includes the following studies: Branched roots, cracked roots, root shape; wild *v.* cultivated root type; three different leaf colors; two flower colors; purple central flower *v.* normal; red, white, yellow, purple, and orange root colors.

At the outset it was observed that inbreeding reduced plant vigor, but the extent of reduction was difficult to learn, because some carrot varieties are genetically fast growing while some are slow growing. A barrier to studying the effect of inbreeding on carotene content was encountered in the difficulty of securing representative carotene samples from individual roots. Carotene is not uniformly distributed throughout the root, but apparently is first deposited at the top of the phloem zone, whence it gradually diffuses to the bottom of the phloem, and then to the top and bottom of the xylem core. After many trials it was learned that the most reliable index of carotene content was a colorimetric reading of the total extracted pigment before separation of carotene and xanthophyll. The correlation between the color reading and milligrams of carotene per 100 g of dry matter is very high. Since the pigment is fairly easily extracted, but the carotene determination is made only with much labor, the method is a valuable aid to carrot breeding for increase of carotene (*6*).

Studies on average root weight of inbred lines, and of hybrids among them, show that the numerous growth factors are segregated to the various lines in a manner corresponding to that for inbred

maize lines. Furthermore, the crossing of enfeebled inbred carrot lines gives the same manifestation of hybrid vigor as in F_1 hybrids of maize inbred lines. Presumably the hypotheses developed for size and weight inheritance in maize are applicable also to carrots, and we may expect important contributions from carrot genetics to the solution of the exceedingly difficult problem of size inheritance. An illustration of production of F_1 generations with excessive hybrid vigor is shown in the following cross between two inbred carrot lines at Davis, Calif. (data unpublished):

Hybrid vigor in a carrot cross

[Average weight, in grams]

Parent lines, A, 34.28; B, 36.42.
Fourth-generation inbred, A, 12.85; B, 24.87.
F_1 hybrid, 80.5.

The variety was Danvers Half Long and parent lines A and B were from strains inbred one generation. A planting of the variety from noninbred seed grown and pulled at the same time had a mean weightof 75 g. Since carrots increase in weight as they grow, it is necessary to pull at the same time all roots that are to be compared.

Some work is being done in California on analysis of root color in carrots.[7] In the cross White Belgian × Yellow Belgian the F_1 generation showed plants with the following different phenotypes:

a. White xylem, lemon phloem, white skin.
b. Lemon xylem, white phloem, white skin.
c. "Ringing" of lemon and white, white skin.

In a cross between an Indian purple carrot (purple phloem) × Commercial Danvers Half Long (orange phloem), the F_1 showed varying degrees of purple.

From the foregoing analysis of Yellow Belgian and White Belgian it is probable that the picture of a simple monohybrid contrast given by Tschermak (*38*) is inadequate.

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IMPROVEMENT OF SALAD CROPS

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THE group of vegetables including lettuce, celery, endive, chicory, cress, parsley, and cornsalad, of which the leaves or stems, or both, are eaten raw, are classed as the salad crops. The production and consumption of these crops, especially lettuce and celery, has increased enormously since their importance as sources of vitamins has become more generally recognized.

The crops of this group are comparatively exacting in their cultural requirements; hence commercial production is limited to areas that, on account of certain environmental conditions, are especially suitable for them. Only the two most important salad crops, lettuce and celery, are grown in large quantity for market.

Most of the cultivated varieties of the salad plants have arisen by selection of individual plants by market and home gardeners. In many cases the parentage and origin are unknown. Only within recent years has an effort been made to improve these crops by scientific methods from stock of known worth.

The salad plants other than lettuce and celery will not be dealt with in the present discussion, as very little work of a scientific nature has been done with the minor crops of this group. The dearth of material on the genetics of the salad plants is no doubt in a large measure due to the difficulties involved in making controlled crosses in many of these species. These plants all produce small flowers that are difficult to handle in securing controlled crosses for genetic studies. Three of them, lettuce, chicory, and endive, are composites, the flowers of which it is difficult, if not impossible, to emasculate, and this makes controlled crossing for genetic studies especially difficult.

The drawings in figure 1 show the structure of a lettuce flower, which is typical of the small-flowered composites. Since the anthers dehisce, or shed pollen, before the stigma appears beyond the sheath, it is necessary to remove the pollen from the stigmas and styles in order to obtain hybrid seed from cross-pollination.

The method of removing the pollen by means of a fine stream of water, first described by Oliver (*4*),[1] is generally employed. By careful washing with water when the individual florets have reached the stage of development shown in figure 1, *D*, it is possible to remove the pollen from the stigmas of most of the florets within the head. By applying the desired pollen to heads depollinated with water, a high percentage of hybrid seed may be obtained from the 15 to 20 ovules within a flower head. A knowledge of the inheritance of a number of

[1] Italic numbers in parentheses refer to Literature Cited, p. 339.

characters that could be identified in the first generation would greatly simplify germ-plasm studies in this group of plants. Many problems in disease resistance and environmental adaptation in the salad crops are awaiting solution by geneticists and plant breeders, and there is need for extended research in this field. Although limited in extent as compared with that on some other crop plants, noteworthy work in practical plant breeding has been done in the salad group.

LETTUCE

Lettuce is the most important salad plant and one of the most important of the vegetable crops. The present commercial crop has

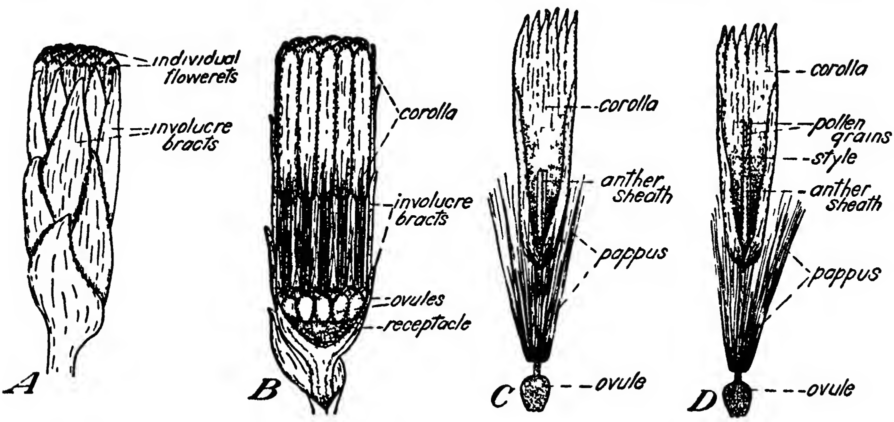

Figure 1.—*A*, The lettuce flower head a few hours before opening. *B*, A longitudinal section through a flower head just before opening, showing structure and arrangement of the individual florets within the involucre. *C*, An individual lettuce floret removed from the head, showing the floral organs. At this stage, a short time before full opening, the stigma is completely enclosed by the anther sheath. *D*, An individual lettuce floret a few minutes later than *C*. The rapidly elongating style has forced the stigma through the apex of the anther sheath. The anthers have already shed pollen, and some of the grains are lodged among the stylar bristles.

an annual value of about $28,000,000. Lettuce is in demand at all seasons of the year and is probably grown under more varied conditions in greenhouses and in field culture than any other vegetable.

Cultivated lettuce is known to botanists as *Lactuca sativa* L. This species has never been found in the wild state but is generally supposed to have been derived from the wild species *L. scariola* L., which is now widely disseminated and is a troublesome weed in many parts of the United States. Lettuce is native to India or central Asia. The time of its introduction into Europe is not known. It is one of the oldest of the vegetable crops. The records of Herodotus, Pliny, Hippocrates, and Aristotle indicate that it was grown as a garden plant in ancient times. It was reported in China as early as the fifth century A. D. Mention of it was made by Chaucer in England in 1340. It was introduced into America from Europe soon after the first colonies were established. Sixteen varieties were listed as being grown in American gardens in 1806.

Lettuce Types and Their Adaptation

Most horticulturists and seedsmen recognize four classes or types of lettuce, namely, crisp-head, distinguished by very firm heads of crisp texture; butter-head, distinguished by soft heads, the inner leaves of which feel oily to the touch; cos, distinguished by elongated heads, stiff leaves, and upright habit of growth; and loose-leaf or bunching, distinguished by loose, nonhead-forming leaves.

The crisp-head and butter-head types, which form round or flattened heads, are often spoken of collectively as "cabbage lettuces" to distinguish them from the "cos lettuces", which form elongated heads. Many good authorities consider that the cabbage and cos lettuces have been derived from two distinct botanical types. However, study of hybrid material from crosses between these two types indicates that they have a common origin.

Since lettuce is comparatively exacting in its environmental requirements during certain periods of its development, large-scale commercial production is limited to areas where climatic conditions are favorable during the critical growth periods. These are regions in which the mean temperatures are comparatively low during the heading period.

The commercial producing area of the United States can be roughly divided into three regions: (1) The western, including the Pacific Coast and Rocky Mountain States of California, Arizona, Colorado, Washington, Oregon, and Idaho; (2) the northeastern, including Massachusetts, New York, and New Jersey; and (3) the South Atlantic, which includes North Carolina, South Carolina, and Florida. On the basis of production the regions rank in the order named. The Western States produce approximately 85 percent of the entire crop.

The Western States grow largely the crisp-head type of lettuce, which sells on the eastern markets as "Western Iceberg." This term is confusing, as it does not refer to the Iceberg variety but applies to the numerous strains of crisp-head lettuce shipped to the markets from the West.

ONE *of the notable examples of practical plant breeding was the development of the Imperial strains of lettuce by the United States Department of Agriculture. Some years ago the lettuce industry in parts of the West, the Imperial Valley in particular, was threatened with ruin by the ravages of two diseases, brown blight and powdery mildew. The Imperial strains have remade the industry in these sections. They are resistant to both blight and mildew, and in certain lettuce-growing areas they now constitute 90 percent of the crop. In addition to their resistance to disease, each strain shows special adaptation to definite regional and climatic conditions.*

Formerly the western crop consisted almost entirely of strains of the variety New York or Wonderful. Much of the acreage formerly planted to this variety is now devoted to the disease-resistant Imperial strains.

Until recently the eastern lettuce crop consisted almost entirely of the butter-head varieties Big Boston and White Boston, also known as Unrivaled. In New York, New Jersey, and the Carolinas the butter-head varieties are being rapidly replaced by strains of crisp-head New York and the Imperials.

There would no doubt have been a more complete change from butter-head to crisp-head type in the East except for the fact that the California strains of crisp-head lettuce have not proved to be adapted to most parts of the East.

This shift from butter-head varieties such as Big Boston to the harder head type of lettuce has resulted from consumer demand. The consuming public has come to prefer the crisp-textured lettuce, and jobbers and dealers find that it stands handling and shipment better than the more delicate butter-head varieties. It has become difficult for eastern growers to find a market for the Big Boston type when the market can be supplied with the crisp New York or Wonderful type.

Cos or romaine lettuce has never been popular in America, although it has long been prized by European gardeners and is grown in home gardens in this country to some extent. There is a limited market for this type of lettuce among the foreign population of the larger cities. Although cos lettuce is coarse in texture, the best varieties are of high edible quality, lacking the bitterness so often present in other types, especially in some of the crisp-head varieties.

The production of loose-leaf or bunching lettuce is largely confined to the home garden and to greenhouse culture during the winter months, when there is considerable demand for this type of lettuce in some localities.

Greenhouse production of lettuce, which at one time constituted an industry of considerable importance, has declined rapidly as field production in the South and West has expanded. Fresh field-grown lettuce can now be obtained at all seasons of the year. A considerable quantity of lettuce is grown under glass during the winter months in the sections around the southern shores of the Great Lakes and near Boston, Mass. The leaf variety Grand Rapids is the most important variety around Cleveland, Ohio. The butter-head variety Belmay is the leading sort in the Boston section.

History of the Important Lettuce Varieties

When Tracy (*6*) published his descriptions of American varieties of lettuce in 1904, more than 100 distinct varieties were recognized. Since that time numerous new names have been added to the list.

Until the recent introduction of disease-resistant strains, to be discussed later, the commercial lettuce crop in the United States consisted largely of two or three varieties. Most of the lettuce reaching the markets from the West consisted of the crisp-head variety New York or Wonderful. The eastern crop consisted largely of the butter-head varieties Big Boston and White Boston.

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Crisp-Head Varieties

New York or Wonderful is a very large, dark-green, solid, late, crisp-head variety. It is the most widely used of all lettuces and has been used as a parent in many of the recently developed strains. The variety was first named and introduced by Peter Henderson & Co. in 1896. Its parentage is unknown.

New York No. 12 is an early strain of a lighter color than the standard variety. It has been one of the most widely adapted crisp-head strains in the East. It was developed by pure-line selection from New York and introduced by the Pieters-Wheeler Seed Co.

New York Special No. 41 is a strain of the New York variety introduced in 1927 by the Ferry-Morse Seed Co., of San Francisco, Calif. It was obtained by pure-line selection from the New York variety. It is especially adapted to conditions in the Imperial Valley.

Imperial F is one of the best of the strains of the New York type resistant to brown blight and mildew. It was developed by Ivan C. Jagger, of the United States Department of Agriculture, from a cross of New York by a cos variety. It was released in 1930. Imperial F is now an important variety in parts of the West where brown blight and powdery mildew are prevalent.

Imperial 615 is a crisp-head lettuce resistant to brown blight, developed by Ivan C. Jagger from a cross between New York and a cos variety. It was first introduced in 1934 and has met with general favor.

Imperial No. 250 was introduced in 1929 by the Ferry-Morse Seed Co. It was obtained by pure-line selection from Jagger's Imperial No. 3. It is a uniform, widely adapted, disease-resistant strain of Imperial.

Hanson is a yellow-green crisp-head variety, a reliable cabbage-heading sort, apparently introduced by the Henry A. Dreer Co., of Philadelphia, Pa., about 1875. Its parentage is unknown.

Mignonette is a dark-green, reddish-brown, crisp-head variety of high quality but too small for a general market lettuce; it is of unknown origin and was first named and introduced in 1895 by Peter Henderson & Co.

The Iceberg variety (which should not be confused with the New York variety, often marketed as Western Iceberg), is a slightly pigmented, yellow-green, crisp-head variety. It is one of the most reliable of the crisp-head types for summer. Iceberg was introduced from Europe and named by W. Atlee Burpee & Co., of Philadelphia, Pa., about 1894.

Malta or Drumhead is one of the largest of all lettuce varieties. It is a coarse, light-green, crisp-head variety forming a loose head, of unknown foreign origin, introduced about 1850.

Denver Market is a very light green crisp-head variety first introduced by F. Barteldes & Co., of Lawrence, Kans., in 1890. Its popularity has been limited to the Middle West.

Butter-Head Varieties

Big Boston is the leading butter-head variety. It is grown in Europe as Trocadero. It has glossy, entire-margined leaves tinged with reddish brown. Its parentage is unknown, but it was first

named and introduced by Peter Henderson & Co. in 1890. Until recently Big Boston was the leading variety in the East.

The variety White Boston or Unrivaled may be described as Big Boston lacking the tinge of red anthocyanin pigment and having slightly lighter green leaves. It was first introduced in this country in 1902. It is believed to be identical with the variety listed by Vilmorin-Andrieux & Cie., of Paris, France, as Sans Rival.

White Boston Cornell No. 43 is a large dark-green strain of White Boston developed by the New York College of Agriculture. It seems to be well adapted for conditions in New York State.

The variety Salamander or Black-Seeded Tennis Ball is one of the most popular of the butter-head varieties. It is one of the oldest varieties of lettuce grown in this country. Its parentage is unknown, but it was introduced from Europe about 1856.

Deacon, one of the older of the American varieties of lettuce of the butter-head type, is distinguishable by its peculiar light gray-green color and its very spreading habit of growth. The variety was named and introduced by the Joseph Harris Co., of Coldwater, N. Y., in 1879.

Wayahead, a more recent addition to the list of lettuce varieties, is a small, early, bright-green, butter-head variety said to thrive under extremely adverse conditions. It was named and introduced by the W. Atlee Burpee Co., of Philadelphia, Pa., in 1908.

Belmay is the leading greenhouse variety in the Boston area. It is a downy mildew-resistant butter-head variety carrying a tinge of reddish brown. It was developed by the Massachusetts Agricultural Experiment Station from a cross between May King and the old reliable forcing variety, Hittinger Belmont. It was introduced in 1928. The variety is discussed later in this article.

Loose-Leaf or Bunching Varieties

Grand Rapids is the most popular of the so-called loose-leaf or nonheading type. It is quite hardy and well adapted for greenhouse culture, but not so well suited for growing out of doors. Grand Rapids was originated and named by Eugene Davis, a market gardener of Grand Rapids, Mich. It resulted from selection from the variety Black-Seeded Simpson. The variety was first introduced into the seed trade in 1890 by D. M. Ferry & Co., of Detroit, Mich.

Early Curled Simpson is a curly, yellow-green, nonheading variety, one of the best of the nonheading sorts for out-of-door culture. It is supposed to have originated about 1865 with a market gardener named Simpson, near Brooklyn, N. Y.

Black-Seeded Simpson is a nonheading variety similar to Early Curled Simpson, but larger and lighter green. Peter Henderson & Co. are said to have introduced the variety about 1880.

Prize Head is probably the best of the loose-leaf or nonheading varieties as regards quality, but is not liked by many on account of its reddish color, which develops especially during cool weather. Its origin is unknown, but apparently it was named and introduced by D. M. Ferry & Co., of Detroit, Mich., about 1868.

Cos or Romaine Varieties

Paris White Cos is the most popular of the cos or romaine type. As a salad lettuce for the home garden it has no superior. It is among the older varieties grown in this country, having been introduced from Europe about 75 years ago, and is considered to be a good variety for warm weather.

Dark Green Cos is similar to Paris White except that the leaves are a darker green. Its parentage and origin are unknown.

Lettuce Breeding

The different producing regions have had their specific problems for the plant breeder. The lettuce industry in some parts of the West, the Imperial Valley of California in particular, was at one time

Figure 2.—**Lettuce plants bagged to prevent uncontrolled pollination. Breeding plots in the Imperial Valley, Calif. Palm trees in middle distance.**

threatened with ruin by the ravages of two diseases, brown blight and powdery mildew. A notable example of practical plant breeding is the development of the mildew and brown blight resistant Imperial strains of lettuce by Ivan C. Jagger, of the United States Department of Agriculture, cooperating with the California growers and shippers. These strains have remade the industry in some sections of the West. They are of the general type of the popular and widely grown variety New York or Wonderful, and in addition to their resistance to disease, each shows special adaptation to certain regional and climatic conditions in the West. The breeding work was started in 1923 at Chula Vista, Calif. A lettuce-breeding plot in the Imperial Valley is illustrated in figure 2.

The strains resistant to both mildew and brown blight were given a letter in addition to the name Imperial. Jagger's other strains have been identified by numbers. The first brown blight-resistant strains released were obtained by selection from the variety New York.

The mildew-resistant strains were obtained by selection from material resulting from crosses between the New York variety and European varieties found by severe tests to be resistant to mildew. In some of the most important lettuce-growing sections of California, these strains now constitute 90 percent of the crop.

Imperial F has already been described. Imperial 13, introduced in 1932, was selected from hybrid material from a cross of New York with the French variety White Chavigne. Imperial 152 and Imperial 615, introduced in 1934, and Imperial 847, released in 1936, were all derived from a cross between New York and a cos variety.

One of the serious problems of eastern lettuce growers is the lack of crisp-head varieties of the New York or Wonderful type that will thrive under eastern soil and climatic conditions. The lack of varieties adapted for the East is explained by the fact that California not only grows more of the commercial lettuce crop than any other State but produces almost the entire seed supply for the United States. This concentration of the production of lettuce seed in California has resulted in the building up, through a long period of selection, of seed stocks especially adapted to western conditions but not to other sections of the country. Western crisp-head varieties almost always fail when tested in the East.

Breeding investigations for the purpose of developing strains of head lettuce of the New York type adapted for eastern conditions was begun by the writer in 1928. The work was begun at the Arlington Experiment Farm, Arlington, Va., and was moved to the United States Horticultural Station at the National Agricultural Research Center, Beltsville, Md., in the spring of 1935. The first strain resulting from this project was released under the name of Columbia No. 1 in the spring of 1936. A similar but earlier strain was introduced in the fall of 1936 as Columbia No. 2. These two varieties were selected from material obtained from a cross made in 1928 between the varieties New York and Hanson. Their chief merit is their adaptability to soil and climatic conditions in some parts of the East.

A third strain introduced in the fall of 1936 as Cosberg is a distinctly new type of head lettuce resulting from a cross of the varieties Iceberg and Paris White Cos. Trial tests of Cosberg show it to be capable of producing solid heads comparatively free of tipburn under conditions that result in severe tipburn in most varieties that will head at a high temperature.

As the breeding work at the Arlington Experiment Farm and the United States Horticultural Station has progressed it has become increasingly evident that the wide range of soils and climate existing in the producing centers of the East will require the development of strains especially adapted to local conditions. For example, it is evident that strains adapted for the muck soils of northern New York State are not likely to prove suitable for the soil and climate of the Carolinas, and that strains adapted for the lettuce section of Florida are not likely to meet the needs of growers in Massachusetts.

Within the last 2 years the Division of Fruit and Vegetable Crops and Diseases, in cooperation with the State experiment stations in New York, Massachusetts, New Jersey, and North Carolina, has undertaken the development of lettuce strains of the crisp-head type

adapted for the particular conditions prevailing in these different sections. The plan is to make available to the State experiment stations the breeding stocks developed at the United States Horticultural Station. In this way it is believed that the large amount of hybrid material now on hand can be used more effectively in securing strains to meet the needs of the several lettuce-growing centers in the East.

Plant breeders are becoming more conscious of the importance of local adaptation of varieties in their crop-improvement work. The needs of widely separated production centers cannot be met by one or two strains of a variety. No one strain is so cosmopolitan that it can adjust itself to such extremes of soil and climate.

Growers of greenhouse lettuce also have problems that have required the attention of the breeder. One of these is the loss from tipburn. This is a physiological break-down of the tissues at the margins of the actively growing leaves. The first appearance of the trouble is characterized by a breaking down of the marginal tissue between the larger veins. The affected area becomes somewhat transparent, loses its green color, and finally becomes brown or blackish. The disease is widespread, occurring wherever lettuce is grown, both under greenhouse and field culture, but it is usually most destructive in greenhouses. It is most likely to appear if high temperature prevails when the plant is in an active stage of growth and especially at the time the plant nears maturity. Much loss is caused by infection of the tipburned tissues by fungus diseases.

The Ohio Agricultural Experiment Station has contributed to the solution of this problem by the development of a strain of Grand Rapids lettuce resistant to tipburn. This is a dark-green, rapidly growing strain, selected from the standard leaf variety, Grand Rapids, and adapted for greenhouse culture.

One of the aims of the breeding work being carried on at the United States Horticultural Station by the Division of Fruit and Vegetable Crops and Diseases is the development of tipburn-resistant strains for field production. The Cosberg variety already released is a step toward the solution of this problem.

Mildew is also a serious problem in the production of lettuce under glass. It has been met by the downy mildew-resistant strain of Grand Rapids developed by Ivan C. Jagger in California, and by the powdery mildew-resistant variety Belmay developed by the Massachusetts Agricultural Experiment Station at Waltham, Mass.

The Jagger strain of Grand Rapids, developed from a cross between Grand Rapids and a cos variety, is a heavier, stalkier strain than the standard variety. It was released in 1936 as Grand Rapids U. S. No. 1.

Belmay is a butter-head type of lettuce adapted for greenhouse forcing. This is a mildew-resistant variety developed by selection from material obtained from a cross between the May King and the old reliable forcing variety Hittinger Belmont, or Hothouse. The cross and preliminary selection work was done by V. A. Tiedjens while he was a member of the staff of the Massachusetts Agricultural Field Station at Waltham. Its resistance to powdery mildew and its adaptation for forcing has made it the leading variety for greenhouse production in the Boston area.

CELERY

Celery ranks next to lettuce in importance as a salad crop. It was one time considered a luxury but is now a common item in the diet of many people.

The production of celery has increased rapidly during the last 10 years. The commercial crop now has an annual value of about $15,000,000. California, Florida, Michigan, New York, New Jersey, Colorado, and Oregon produce almost the entire celery crop of the country.

Celery (*Apium graveolens* L.) is a biennial plant native to the low marshlands of southern Europe, northern Africa, and southwestern Asia. A wild form is native in the southwestern United States. Although the plant was known to ancient peoples, recorded history indicates that it was not used as an article of food until modern times. Its development as a garden plant began among the gardeners on the lowlands of Italy and spread to France and England. By selection the undesirable wild plant, long considered poisonous, has been transformed into a crisp, sweet, appetizing, and wholesome item of food.

The commercial producing areas are even more limited than in the case of lettuce. The production of the early yellow type of celery is centered in the Sacramento district of California, the Sanford district of Florida, and the Kalamazoo district of Michigan.

Winter or green celery is produced in the market-garden sections around Great Salt Lake, Utah, Denver, Colo., Boston, Mass., and the trucking sections of New York, New Jersey, Michigan, and Pennsylvania.

History of Celery Varieties

There are two distinct types of celery—(1) yellow or summer celery, of which the variety Golden Self-Blanching is typical, characterized by its early maturity and ease of blanching, and (2) green or winter celery, of which Giant Pascal is typical, maturing later and having greater weight and better quality than the early yellow type. The yellow type can be blanched in the field as it stands in the row by excluding light merely by means of paper or boards. The green or winter varieties are more difficult to blanch. The plants must be either banked with soil as they stand in the row so that only the tips of the leaves are exposed to light or they must be dug and placed in light-proof pits to destroy the green coloring of the petioles.

Most of the old standard celery varieties—such as Golden Self-Blanching, Giant Pascal, White Plume, and Winter Queen—are of unknown parentage and origin.

Yellow Varieties

Golden Self-Blanching is one of the oldest of the yellow celery varieties. It has long been a standard variety in France and was very likely introduced to the United States from Europe. Its parentage is unknown. For many years French-grown seed of this variety was considered to be superior to American-grown stocks. Good strains of American-grown seed are now available. There are both tall and dwarf strains of this popular variety.

Easy-Blanching is a tall yellow celery resembling Golden Self-Blanching but a little later in maturing and having bright rich green

foliage. It is claimed that Easy-Blanching is hardier and more resistant to blight than Golden Self-Blanching.

White Plume is the earliest and most easily blanched of all celery varieties. The blanched petioles are snowy white. Most strains of this variety have the weakness of not keeping well after digging.

Golden Plume is one of the best of the early varieties. It is somewhat resistant to blight and keeps well in storage. The plants are medium in size, compact, and stocky. It is earlier, stalkier, and more vigorous than Golden Self-Blanching.

Some of the more recently developed yellow varieties include the yellows-resistant Michigan Golden and Curly Leaf Easy-Blanching, introduced by the Michigan Agricultural Experiment Station in 1933 and 1936, respectively; Non-Bolting Golden Plume, Golden Pascal, Crispheart, and Golden Supreme, developed and introduced by the Ferry-Morse Seed Co.

Green Varieties

Giant Pascal is one of the oldest of the green varieties. It is considered the standard of excellence in celery. The plants are tall and have rich dark-green foliage. The large thick petioles when blanched in soil are tender and crisp and have a rich nutty flavor. It is probably of European origin.

Winter Queen is a dark-green dwarf celery resembling Golden Self-Blanching in habit of growth. It matures earlier and is more easily blanched than Giant Pascal. It is probably an American variety, although its parentage is not known.

Fordhook is one of the best of the winter celery varieties, having good keeping qualities. The plants are somewhat dwarf in habit of growth, and the petioles are thick and heavy. It was named and introduced by the W. Atlee Burpee Co., of Philadelphia, Pa., in 1915.

A recent addition to the list of green varieties of celery is Utah. This is a strain of winter celery developed by the Chinese gardeners around the Great Salt Lake in Utah. The strain has also been called Chinese celery. It is a green celery of high quality, a week to 10 days later than Giant Pascal. The variety seems to be well adapted for some of the irrigated sections of the West.

Recent Celery Improvement

Celery growers look to the plant breeder for the solution of some of their most serious problems. Among these are the celery yellows disease, premature seedstalk development, pithiness, and obtaining earlier maturity.

Some of these problems have already been attacked by plant breeders and much has been accomplished in reducing losses.

Celery yellows first became a serious disease in Michigan. It was first observed there in 1914 and has since been found in Ohio, Pennsylvania, New York, New Jersey, Massachusetts, and Connecticut. Only the yellow celery varieties are susceptible, the green varieties being immune. Plants having the disease lose their normal color and become stunted; the tissues are brittle and have a bitter taste. The disease is caused by a species of *Fusarium* which remains in the soil and gradually becomes more abundant as celery is grown on the same land year after year.

The first attempt to solve the yellows problem by breeding methods was initiated by G. H. Coons and Ray Nelson, of the Michigan Agricultural Experiment Station. The work was later carried on by Ray Nelson and L. C. Cochran. The first strains released were resistant to yellows but were found to be too green to blanch easily. In 1933 the Michigan Golden Yellows Resistant strain was introduced. It was obtained by selection of yellows-resistant plants from a tall strain of Golden Self-Blanching.

The Michigan station has also introduced a yellows-resistant selection from the Newark Market variety. It was released in 1936 as Curly Leaf Easy-Blanching.

Some strains of celery shoot to seed prematurely if the plants are subjected to low temperature during the early growth period. In seasons when cold weather prevails after the plants have been set in the field or in cases where the seedlings in the plant-growing beds are subjected to low temperature, a heavy loss results from premature seeding. Emsweller (*3*) demonstrated the possibility of avoiding this trouble by breeding nonbolting strains.

The new Non-Bolting Golden Plume variety, developed by the Ferry-Morse Seed Co., and introduced in 1936, is a step toward the solution of this problem. The new strain was obtained by pure-line selection from the variety White Plume. The chief merit of the strain is its resistance to premature seedstalk formation under conditions that induce early seeding in many of the commercial varieties of early celery.

Pithiness in celery, a condition in which the parenchyma cells collapse, resulting in hollow, spongy petioles or stalks, has been shown by Emsweller (*2*) to be an inherited character. The establishment of the genetic basis of pithiness paves the way for the development by scientific breeding of strains free from this undesirable character.

The superior quality of green celery of the Giant Pascal type has long been recognized. On the other hand, the early yellow celery has the distinct advantage of being much more easily blanched than the green type. A celery combining the high quality and heavier stalks of the green celery with the early maturity and easy blanching characters of the yellow type would be a worth-while breeding accomplishment. The Ferry-Morse Seed Co. claim to have approached this in their new strain of Golden Pascal. It is a dark-green selection from Golden Plume.

The New York State College of Agriculture has investigations on celery breeding and genetics in progress but has as yet released no new strains.

GENETICS OF SALAD CROP PLANTS [2]

VERY little is yet known of the inheritance of characters in the salad crop plants. Some investigations have been made on the inheritance of certain characters in lettuce and in celery, but the genetics of only a few of these is known as yet.

[2] This section is written primarily for students and others professionally interested in breeding or genetics.

Lettuce

The most comprehensive study of the germ plasm of a salad crop plant is that made on lettuce by Durst (*1*). His investigations included the inheritance of plant height, time required for flower production, habit of growth, anthocyanin in the leaves and ray flowers, prickles on stems and leaves, seed color, leaf length, leaf width, and leaf area. Both cultivated varieties of *Lactuca sativa* and the wild form, *L. scariola*, were used in his studies.

Durst found anthocyanin in the leaves and ray flowers to be inherited as a single factor dominant to the absence of the pigment. Black seed behaved as if inherted via a single factor dominant to white seed. Prickles on the midrib of the leaves and on the stems are also inherited as a single factor dominant to the absence of prickles.

The inheritance of lobed leaves characteristic of some forms of the wild species *Lactuca scariola* is apparently controlled by complementary factors. The F_2 progenies from crosses of lobed with entire-margined leaf types gave approximately nine lobed to seven entire-margined.

Leaf length, leaf width, leaf area, time required for flower production, plant height, and habit of growth behaved as quantitative characters, and their inheritance is controlled by many factors.

Thompson [3] has determined the inheritance of certain color characters in lettuce. A report is made on the inheritance of three distinguishable anthocyanin pigment types in the leaves, of dark-green and yellow-green chlorophyll color, of seed color, and of a chlorophyll deficiency that does not follow Mendelian inheritance.

The three anthocyanin pigment types in the leaves of lettuce studied by Thompson were the full red type characteristic of the variety Mignonette, the spotted type characteristic of the variety California Cream Butter, and the tinged type characteristic of the variety Iceberg.

The inheritance of these three anthocyanin types was found to be controlled by a multiple allelomorphic series of three genes and two pairs of complementary genes. The presence or absence of the pigment is controlled by the complementary genes and the intensity and pattern by the multiple allelomorphic series.

Dark-green chlorophyll color, characteristic of the variety New York, was found to behave as a single factor dominant to the gene for yellow-green characteristic of the variety Hanson.

Studies on seed color confirm the results obtained by Durst that black seed is due to a single gene dominant to the gene for white seed.

The chlorophyll deficiency in the leaves of lettuce studied by Thompson was found to be non-Mendelian in inheritance. The deficiency was inherited only through the deficient portions of the mother plant,and its inheritance was not affected by the type of pollen applied.

Celery

The inheritance of pithiness in celery has been studied by Emsweller (*2*) in the variety Utah. Emsweller isolated inbred lines from this variety that were homozygous for solid petioles free from pithiness.

[3] Thompson, R. C. Genetic relations of some color factors in lettuce (In manuscript; intended for publication as U S. Dept. Agr. Tech Bull)

Progenies from heterozygous lines segregated approximately three pithy to one nonpithy. The results obtained indicate that pithiness in celery is controlled by a single factor, dominant to the recessive condition of solid or nonpithy petioles.

It should be noted here that the problem of pithiness in celery was practically solved by Sandsten and White (*5*) in 1900. They observed that certain stocks of plants of the variety Golden Self-Blanching from different sources varied greatly in the percentage of pithy plants produced. Strains of both American- and French-grown stocks were tested. Lots from the French-grown seed showed much less pithiness on the average than lots from the American-grown seed. Some of the French stocks were entirely free of pithiness, which White and Sandsten, who reported the work, attributed to more careful selection of seed stocks by French growers. Although Sandsten and White's results strongly indicated an inherited difference in strains in respect to pithiness, they failed to carry their investigations far enough to show a definite genetic relationship.

Premature seedstalk development in celery has also been studied by Emsweller (*3*). The varieties Golden Plume and Golden Self-Blanching were used. Emsweller was able to isolate strains homozygous for the nonbolting habit, which would not bolt under conditions causing a high percentage of bolting in other strains. He was able to isolate some lines that were strongly annual in their seeding habit, some plants of which seed prematurely even under favorable conditions for vegetative growth. It is evident from his results that premature seedstalk development in celery is inherited. He concluded that nonbolting is a quantitative recessive character. The influence of environment on the expression of the bolting character makes genetic analysis of it difficult.

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See footnote 3, p 338.

IMPROVEMENT OF VEGETABLE CROPS—APPENDIX

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THE appendix to these articles on vegetable improvement consists of four tabulations of information as follows:

1. A list of vegetable varieties developed by State and Federal research agencies and released by them for commercial use.

2. A list of vegetable strains, varieties, and breeding stocks or groups of the same that are in the hands of State and Federal research workers and which have some special merit, or are of practical or theoretical interest as breeding material. It should be noted that material listed in table 1 is not repeated in table 2, although practically without exception introducers of varieties all maintain some stock of their introductions. Table 2 should properly include all material listed in table 1.

3. A list of vegetable breeding and improvement activities in the United States by States and crops.

4. A brief summary of vegetable breeding and improvement activities in countries other than the United States.

The data in these tabulations and summaries were obtained through a questionnaire sent to all vegetable crop research agencies in this country and to a large number in other lands. The writers of the present articles are grateful for the generous help of their fellow workers, both here and abroad, in making this compilation possible. Despite the great amount of data submitted and the generous response to our requests, it is known that these appended tables do not contain all of the data that could well be included. Some of the workers interrogated were perhaps too modest to list certain cultures as being important or of interest to others; others were admittedly too pressed by other matters to prepare a detailed list of their material and activities. But even though the data are incomplete, the reader will find clues to nearly every kind of vegetable-breeding material that is available and leads to the numerous investigators who are engaged with the hundreds of breeding and improvement problems that are receiving attention today.

The writers hoped that it would be possible to include similar tables of information relating to private work by commercial seedsmen. The immensity of the task of determining the origin of the hundreds of varieties made it impossible. A few commercial firms keep rather complete records of the parentage and dates of their introductions, but most do not. The major role that has been played by private agencies has been repeatedly referred to in these articles, and acknowledgment made to individuals and firms wherever pertinent information could be included. It should thus be clear to all that no discrimination is intended by the omission of more extensive data on commercial contributions. Unfortunately, justice cannot be done to such a task within the space available here.

Table 4.—*Improved varieties and strains of vegetable crops, peanuts, and sweet corn developed and released by State and Federal research agencies*

BEAN

Station or U S Department of Agriculture	Crop	Variety name	Date introduced	Parents	Breeding method	Superior characters
Alabama	Bean	Alabama No 1 (pole, snap)	1933	Unknown	Selection	Heavy yield, bears over the length of the vine and over long season, resistant to nematode
	do	Alabama No 2 (pole snap)	1933	do	do	Heavy yield mature beans keep well in the field, nematode resistant
Connecticut (State)	do	Connecticut Fordhook (lima)	193	Fordhook	Pure line selection	High yield
Idaho	do	Idaho Refugee (snap)	1934	Stringless Refugee × Corbett Refugee	Hybridization	Vigor, resistant to bean mosaic, 1 week earlier than Stringless Refugee
	do	Great Northern U I No 81 (field)	1932	Commercial Great Northern	Pure line selection	Productivity, uniformity, resistant to common bean mosaic
	do	Great Northern U I No 59 (field)	1936	do	do	Larger bean than No 81, 3 days earlier in maturity
	do	Great Northern U I No 123 (field)	1936	do	do	Do
Illinois	do	Large Podded Henderson Bush (lima)	1935	Henderson Bush	Cross between two Henderson Bush selections	Large Podded early, productive under Illinois conditions
	do	Baby Potato Lima	1936	do	Selected out of Henderson Bush probably an accidental cross	Henderson Bush vine and earliness, with small thick potato-type beans, crowded in pods Outyields Henderson
Maine	do	Highmoor Old Fashioned Yellow Eye (field)	1928	Old Fashioned Yellow Eye	Selection	Higher yield more uniform and attractive pattern
Massachusetts	do	Waltham Scarlet (horticultural)	1935	French Horticultural	do	Bright scarlet broad, long pods, high yield
Michigan	do	Robust (field)	1913	Navy Pea	do	Immune to common bean mosaic
New York (Cornell)	do	Perry Marrow (field)	1918	White Marrow × Wells Red Kidney	Hybridization	Anthracnose resistant, yield
	do	Genesee (field)	1918	Robust × Wells Red Kidney	do	Anthracnose resistant root rot resistant
	do	Honeoye (field)	1918	do	do	Do
State (Geneva)	do	Geneva Red Kidney (field)	1928	do	do	Blight resistant, free from hard shell
	do	York Red Kidney (field)	1928	do	do	Do
Department	do	U S No 1 (snap)	1933	Wells Red Kidney × Stringless Green Refugee	do	Early, mosaic and drought tolerant
	do	U S No 2 (lima)	1933	Henderson Bush Lima	Selection	Early, matures evenly, high yield
	do	U S No 3 (pole, snap)	1934	World Wonder	do	Rust resistant, stringless, Kentucky Wonder type, round podded
	do	U S No 4 (pole snap)	1934	Phenomenon Pole	do	Rust resistant, large podded, high yield
	do	U S No 5 (snap)	1935	U S No 1 × Corbett Refugee	Hybridization	Mosaic resistant, early, long pods, good yield determinate growth

Table 4.—*Improved varieties and strains of vegetable crops, peanuts, and sweet corn developed and released by State and Federal research agencies*—Con.

BEAN—Continued

Station or U. S. Department of Agriculture	Crop	Variety name	Date introduced	Parents	Breeding method	Superior characters
Virginia	Bean	32-C-4 (pole, snap)	1934	Kentucky Wonder × Brockton Pole.	Hybridization and selection.	Rust resistant, prolific and superior quality of pod.
	do	17-B (pole, snap)	1934	do	do	Do.
	do	17-A (pole, snap)	1934	do	do	Do.
	do	14-A (pole, snap)	1934	Kentucky Wonder × Horticultural Pole.	do	Do.
	do	11-A (pole, snap)	1934	do	do	Do.
	do	5-A (pole, snap)	1934	Powell Prolific × Marblehead Pole.	do	Do.
	do	34-B (pole, snap)	1934	do	do	Do.
	do	32-B (pole, snap)	1934	Kentucky Wonder × Marblehead Pole.	do	Do.
Wisconsin	do	Wisconsin Refugee (snap)	1934	Stringless Green Refugee × Corbett Refugee.	Hybridization	Resistant to bean mosaic.

LEAFY CROPS

Station or U. S. Department of Agriculture	Crop	Variety name	Date introduced	Parents	Breeding method	Superior characters
California	Spinach	California Canner 159	1929	Prickly Winter	Selection	Early, productive.
	do	California Canner 195	1929	do	do	Do.
Georgia	Cabbage	Cabbage-Collard	1911	Blue Stem Collard × Charleston Wakefield Cabbage.	Hybridization	Semiheads of good quality
Louisiana	do	Louisiana Copenhagen	1934	Copenhagen Market	Pure-line selection—inbreeding and intercrossing, 5 generations of selected lines.	Uniformity; resistant to boring; compact head; short, stout core; excellent quality.
	Collard	Louisiana Sweet	1934	Georgia Collard	Inbreeding	Improved uniformity; short petiole; compact rosette; more leaves. Free of purple plants. Good quality.
Maryland	Spinach	Maryland Savoy	1935	Virginia Savoy	Mass selection	Winter hardiness.
Massachusetts	Lettuce	Bel-May	1928	May King × Belmont	Hybridization	Downy mildew resistant, good head, fast growth.
Michigan	Celery	Michigan Golden	1933	Golden Self Blanching	Single-plant selection	Resistant to celery yellows.
	do	Curly-Leaf Easy Blanching.	1926	Newark Market	do	Immune to celery yellows; will blanch in cold storage; high-quality easy-blanch type.
New York (Cornell)	Cabbage	Early Danish	1925	Commercial Danish	Selection	Early; short core; good quality.
	do	Green Sugar Loaf	1930	Red × Jersey Wakefield	Hybridization	Table quality.
	do	Purple Sugar Loaf	1930	do	do	Do.
	do	Magenta	1933	Danish Round Red	Selection and hybridization.	New color; good quality.
	do	Early Savoy [1]	1934	Commercial Savoy	Selection	Uniformity.

	do	Jersey Wakefield [1]	1932	Commercial Jersey	do	Do
	do	Glory [1]	1933	Commercial Glory	do	Uniformity yield
	do	All Head Early [1]	1934	Commercial Succession	do	Uniformity, type
	do	Succession [1]	1934	do	do	Uniformity, yield
Ohio.	Lettuce	Grand Rapids (Tipburn Resistant)	1933	Grand Rapids	do	Tipburn resistant, light color, very heavy
Pennsylvania	Cabbage	Penn State Ballhead	192	Unknown	Line selection	Uniformity of type good keeping qualities and high yield
Department	Lettuce	Imperial F	1930	New York × Cos	Hybridization	Immune to brown blight, shows special adaptations to certain regional and climatic conditions in the West
	do	Imperial 13	19[illegible]2	New York × White Chavigne	do	Do
	do	Imperial 152	1934	New York × Cos × (?)	do	Do
	do	Imperial 615	1934	New York × Cos	do	Do
	do	Imperial 847	1936	do	do	Do
	do	Grand Rapids U. S. No 1	1936	Grand Rapids × Cos	do	Some resistance to powdery mildew, heavier, stockier plants than Grand Rapids
	do	Columbia No 1	1930	New York × Hanson	do	Superior heading qualities under eastern conditions Slow to shoot to seed
	do	Columbia No 2	1936	do	do	Earlier than Columbia No 1, adapted for spring crop in eastern United States
	do	Cosberg No 1	1936	Paris White Cos × Iceberg	do	Tipburn and heat resistant, high edible quality, free from bitterness
Virginia (Truck sta)	Kale	V. T. E. S. Scotch	19[illegible]	Dwarf Blue Curled Scotch	Pure line selection	More resistant to cold, more curled, retains dark green color after periods of low temperatures
	Spinach	Virginia Savoy	1920	Unnamed Manchurian variety × Bloomsdale Viroflay, and Long Standing	Hybridization (natural) and selection	Resistant to mosaic and low temperature Rapid growing in fall
	do	Old Dominion	1930	Virginia Savoy × King of Denmark	Hybridization	Similar to Virginia Savoy but slower in bolting to seed in spring
Wisconsin (in cooperation with department)	Cabbage	Wisconsin Hollander	1916	Danish Ballhead	Mass selection	Resistant to yellows
	do	Wisconsin Brunswick	1917	Fottlers Brunswick	do	Do
	do	Wisconsin All Seasons	1920	All Seasons	do	Do
	do	Marion Market	1925	Copenhagen Market	Pure line selection	Do
	do	All Head Select	1925	All Head Early	do	Do
	do	Globe	1925	Glory of Enkhuizen	do	Do
	do	Jersey Queen	1931	Jersey Wakefield	do	Do
	do	Wisconsin Ballhead	1935	Danish Ballhead	do	Do
	do	Racine Market	1935	Copenhagen Market	do	Do
	do	Resistant Red Hollander	1924	Red Hollander	Mass selection	Do

[1] Specially selected strains derived from existing varieties named

TABLE 4.—*Improved varieties and strains of vegetable crops, peanuts, and sweet corn developed and released by State and Federal research agencies*—Con

Station or U S Department of Agriculture	Crop	Variety name	Date introduced	Parents	Breeding method	Superior characters
			PEA			
Maryland	Pea	Maryland Alaska	1932	Alaska	Mass selection	Fusarium wilt resistant
Wisconsin	do	Badger	1921	Horsford × French June	Hybridization	Small seed high quality good production
	do	Alcross	1922	Cross between two Alaska strains	do	Early maturity resistant to wilt
	do	No 19 Alaska	1922	do	do	Do
	do	Hustler	1922	Notts Excelsior × Horsford	do	Early maturity pitted round
	do	Horal	1923	Horsford × Alaska	do	Small seed wrinkled hardy wilt resistant
	do	Ashford	1924	Horsford selection	Pure line selection	Short blossoming period good quality
	do	Acme	1925	Horsford × French June	Hybridization	Vigor good quality wrinkled seed
	do	Primal	1925	Alaska × Surprise	do	Wrinkled high quality vigor
	do	Wisconsin Early Sweet	1931	Resistant Alaska × Surprise	do	High quality and vigor resistant to wilt
	do	Wisconsin Perfection	1933	Original cross Arthur × Perfection and backcrossed to Perfection	do	Vigor high quality resistant to wilt
	do	Wisconsin Penin	1936	Horal × Prizewinner	do	Large seeded high quality 4 days or more earlier than Perfection in maturity fully resistant to wilt
			TOMATO			
California	Tomato	Pearson	1936	Fargo × California 55	Hybridization	Determinate vine tough skin intense color
	do	California 55	1928	Santa Clara	Inbreeding	Smooth fruit high yield intense color
Georgia	do	Hastings Everbearing Scarlet Globe	1932	Globe × Burpee	Hybridization	Resistant to fusarium wilt and leaf diseases tolerates hot weather and drought better than most varieties
Illinois	do	Lloyd Forcing	1930	Louisiana Pink × Grand Rapids	Crossing followed by selection	Wilt resistant greenhouse type
	do	Blair Forcing	1930	do	do	Do
	do	Urbana Forcing	1936	Marglobe × Grand Rapids	do	Do
	do	Sureset Forcing	1936	Urbana Forcing × Blair Forcing	do	Do
	do	Long Calyx Forcing	1936	Lloyd Forcing × Marglobe	do	Do
	do	Illinois Pride	1936	New Century	Selection	Wilt resistant canning type

	do	Early Baltimore	1936	Indiana Baltimore	do	Wilt-resistant canning type, especially adapted to high-nitrogen prairie soils.
	do	Prairiana	1936	Marvana	Selection out of a mutation or accidental cross.	Do.
	do	Illinois Baltimore	1936	Indiana Baltimore	Selection	A wilt-resistant Baltimore.
Indiana	do	Indiana Baltimore	1919	Greater Baltimore	do	High yield; foliage protection, resulting in better color.
Louisiana	do	10-4	1936	Louisiana Pink × Walter Richards	Crossing and back-crossing; growing plants on wilt plots.	Few small seed. Resistant to wilt and somewhat resistant to early blight; pink; adaptability to Louisiana conditions.
Maryland	do	Maryland Canner	1928	Unknown	Selection	Solidity of flesh.
	do	Maryland Slicer	1930	Italian Pear × Greater Baltimore.	Hybridization	Do.
	do	Hybrid No. 4	1932	Greater Baltimore × San Jose Canner	do	Do.
Massachusetts	do	Waltham Forcing	1931	Unknown	Single-plant selection	High yield, sets fruit under adverse conditions; good color.
Michigan	do	Michigan State Forcing	1935	Marglobe × Ailsa Craig	Hybridization	Self-pollinating, high quality, wilt resistant.
	do	John Baer	1926	John Baer	Single-plant selection	High yield, good market and canning qualities.
Minnesota	do	533	1935	Viking × Bonny Best	Hybridization	Early, productive.
	do	29-35	1936	Unnamed	do	Early, high color and fruit quality.
New Jersey	do	Rutgers	1934	Marglobe × J. T. D.	do	Inside color ripens from center; flavor for juice.
New York (State)	do	Geneva John Baer	1930	John Baer	Selection	Earliness, deep red color.
	do	Nystate	1935	Ponderosa × King Humbert	Hybridization	Earliness, large size, smooth fruit, deep red color.
North Dakota	do	Red River	1925	Earliana × Sunrise	do	Earliness, smooth form, early. Adapted to Great Plains area.
	do	Bison	1929	Red River × Cooper Special	do	Early, determinate, heat resistant. Adapted to Great Plains area.
	do	Fargo Yellow Pear	1932	Bison × Yellow Pear	do	Early, determinate. Adapted to Great Plains area.
	do	Pink Heart	1932	Bison × Ohio Red	do	Do.
	do	Golden Bison	1932	Bison × Golden Queen	do	Do.
	do	Early Jumbo	1929	June Pink × Globe	do	Early, large size. Adapted to Great Plains area.
	do	Farthest North	1934	Bison × Red Currant	do	Extreme earliness. Adapted to Great Plains area.
Ohio	do	Marhio	1930	Marglobe	Selection	Resistant to fusarium wilt. Scarlet-red fruit, productive.
Pennsylvania	do	Nittany	1922	Enormous × Yellow Pear	Hybridization	Yield and uniformity.
	do	Matchum	1922	Hummer × Matchless	do	Do.
	do	Penn State Earliana	1926	Earliana	Selection	Earliness, uniformity, yield.
	do	Penn State	1935	Burpee Self-Pruning × Penn State Earliana.	Hybridization	Earliness, shape, and uniformity of fruit and yield. Determinate foliage.
Puerto Rico	do	LJX-7	1935	Louisiana Pink × native	do	Tolerance to bacterial wilt.

TABLE 4.—*Improved varieties and strains of vegetable crops, peanuts, and sweet corn developed and released by State and Federal research agencies*—Con.

TOMATO—Continued

Station or U S Department of Agriculture	Crop	Variety name	Date introduced	Parents	Breeding method	Superior characters
Tennessee	Tomato	Tennessee Pink		Unknown	Mass selection	Fusarium wilt resistant
Department	do	Tennessee Red	1912	Beauty	do	Do
	do	Norton	1917	Stone	Selection	Do
	do	Marvel	1918	Merveille de Marchés	do	Fusarium wilt and nailhead resistant
	do	Columbia	1918	Greater Baltimore	do	Fusarium wilt resistant
	do	Arlington	1918	do	do	Do
	do	Norduke	1922	Norton × Duke of York	Hybridization	Do
	do	Marvana	1924	Marvel × Earliana	do	Do
	do	Marvelosa	1924	Marvel × Ponderosa	do	Fusarium wilt and nailhead resistant
	do	Marglobe	1925	Globe × Marvel	do	Do
	do	Break o' Day	1931	Marglobe × Marvana	do	Do
	do	Pritchard [2]	1932	Cooper Special × Marglobe	do	Resistant to fusarium wilt, nailhead, and cracking
	do	Glovel [2]	1935	Globe × Marvel		
Washington	do	Seedling No 36	1930	Bonny Best × Best of All	Hybridization	Heavier producer than parents Good shipper
	do	Seedling No 50		do	do	Heavier producer than parents

CUCURBITS

Station or U S Department of Agriculture	Crop	Variety name	Date introduced	Parents	Breeding method	Superior characters
California	Watermelon	California Klondike	1933	Klondike	Inbreeding	Uniformity, flesh color, edible quality
	do	Long Mountain	1936	Stone Mountain	do	Oblong type, adapted to shipping
	do	Striped Klondike	1936	Striped Klondike	do	Uniformity, high sugar
	do	Resistant Klondike No 7	1936	Iowa Belle × Klondike	Hybridization	Wilt resistant
	Bush squash	Grey Zucchini No 1	1936	Zucchini	Inbreeding	Early, productive small, single-stem plant
	Cantaloup [3]	Powdery Mildew Resistant Cantaloup No 1	1931 1931	Resistant variety from India and several commercial varieties	Hybridization	Resistant to powdery mildew
	do	Powdery Mildew Resistant Cantaloup No 50	1932	do	do	Do
	do	Powdery Mildew Resistant Cantaloup No 50-15	1933	do	do	Do
	do	Powdery Mildew Resistant Cantaloup No 45	1935	Hale Best × unfixed variety from India	do	Resistant to powdery mildew edible quality Superior shipping qualities
	Honey Dew melon	Powdery Mildew Resistant Honey Dew No 60	1934	Unfixed variety from India × Honey Dew × Honey Ball	do	Resistant to powdery mildew, edible quality

Connecticut (State)	Squash	Connecticut Straight Neck	1936	Straight Neck Inbred × Giant Summer Crook Neck	do	Early, productive, uniform, smooth
Florida	do	African	1935		Introduction	High quality and yield in Florida, some resistance to stem borers
	Watermelon	Leesburg	1936	Kleckley Sweet	Pure line selection on wilt infested soil	Resistant to fusarium wilt in Florida
Iowa	do	Iowa King	1930	Conqueror × (²)	Hybridization	Resistant to fusarium wilt
	do	Iowa Belle	1930	Conqueror × Kleckley Sweet	do	Do
	do	Pride of Muscatine	1930	Kleckley Sweet	Selection	Do
	Squash	Des Moines		Des Moines	Inbreeding	Uniformity and quality
Maryland	Muskmelon	Maryland Gem	1928	Buskirk s Gem	Selection	Thick, yellow flesh quality
Michigan	Cucumber, pickling	National Pickle	1929	Snow Pickling	Single plant selection massing of selfed lines	High yield, superior pickling quality
Minnesota	Squash	Kitchenette	1930	Green Hubbard	Inbreeding	Uniformity family size
	do	New Brighton	1932	do	do	Uniformity large size
	do	1 35	1935	Buttercup	do	Early high quality, family size, stores well
	Cucumber	454 35	1935		Introduction and inbreeding	Early, productive pickling type
	Watermelon	Northern Sweet	1932		do	Early, high quality, productive
New York (State)	Cucumber	Geneva	19[illegible]	Arlington White Spine × Rochford Market	Hybridization	Parthenocarpic
North Dakota	Squash	Buttercup		Quality × Essex hybrid (²) (natural cross)	Inbreeding	Convenient size, high quality, easily prepared
Department	Cantaloup [4]					
	Watermelon	Conqueror	1911	Eden × Stock citron	Hybridization	Resistant to fusarium wilt
Vermont	Squash	Vermont Hubbard		Hubbard	Inbreeding	Improved uniformity and culinary quality

SWEET CORN

Connecticut (State)	Sweet corn	Spancross C2	1933	Spanish Gold × C2	Hybridization	First early hybrid, large ear resistant to bacterial wilt
	do	Spancross P39	1933	Spanish Gold × P39	do	Second early resistant, good quality
	do	Marcross C6	1933	G E Market × C6	do	Very large ear, first early, resistant
	do	Marcross C13 6	1935	C13 × C6	do	Do
	do	Marcross C13 2	1935	C13 × C2	do	Do
	do	Marcross P39	1935	G E Market × P39	do	Second early, very large ear, good quality resistant
	do	Whipcross C6 2	1933	C6 × C2	do	Midseason, large ear, resistant
	do	Whipcross C7 2	1933	C7 × C2	do	Midseason, large ear, narrow kernel, quality
	do	Whipcross P39 C2	1933	P39 × C2	do	Midseason, large ear, resistant to bacterial wilt
	do	Whipcross P39	1933	Whipple × P39	do	Midseason large ear, good quality, resistant
	do	Redgreen	1926	C78 × C77	do	White, good quality, sun red leaves
	do	M Spanish Gold	1935	Spanish Gold	Synthetic variety	Very early, parent of first early hybrid
	do	M G E Market	1935	G E Market	do	Early, resistant to bacterial wilt
	do	M Whipple	1935	Whipple	do	Midseason, resistant to bacterial wilt

[2] In cooperation with Florida station

[3] In cooperation with U S Department of Agriculture

[4] See California, above

TABLE 4.—*Improved varieties and strains of vegetable crops, peanuts, and sweet corn developed and released by State and Federal research agencies*—Con.

SWEET CORN—Continued

Station or U S Department of Agriculture	Crop	Variety name	Date introduced	Parents	Breeding method	Superior characters
Florida	Sweet corn	Florida No 191	1934	Country Gentleman, Cuban Flint, Loveless, Pope and Stubbs	Hybridization inbreeding bulk crossing of inbreds and selection	Husk protection and good table quality
	do	Suwannee Sugar	1935	Southern Snowflake ¾, Long Island Beauty ¼	Hybridization and one back cross to Snowflake, selection	Husk protection, southern plant type, good quality
Illinois	do	Illinois Narrow Grain Evergreen				
	do	Inbred No 13	1935	Narrow Grain Evergreen	Best open pollinated strains first selected by ear row methods, followed by inbreeding and a high degree of selection within each line, then tested out in numerous crosses	Cross 14×13 is a high yielder available commercially in 1937
	do	Inbred No 14	1935	do	do	Do.
	do	Country Gentleman	1925	Country Gentleman	Ear row selection	Yield, uniformity, canning quality, adaptability to Illinois
	do	Narrow Grain Evergreen	[5]1925	Narrow Grain	do	Do
	do	Illinois Country Gentleman	1935	Country Gentleman	Same as for Illinois Narrow Grain inbreds	Yield, uniformity, canning quality, adaptability to specific Illinois conditions
	do	Inbred No 1	1935	do		Do
	do	Inbred No 3	1935	do		Do
	do	Inbred No 5	1935	do		Do
	do	Inbred No 6	1935	do		Do
	do	Inbred No 8	1935	do		Do
	do	Inbred No 9	1935	do		Do
	do	Inbred No 10	1935	do		Do
	do	Inbred No 15	1935	do		Do
	do	9 hybrids		do	Same as for Illinois Narrow Grain inbreds	Do
Maryland.	do	Hopeland	1920	Stowell Evergreen × Johnson County White	Hybridization	Productivity
North Dakota	do	Sunshine	1924	Golden Bantam × Gill s Early Market	Hybridization, selfing, followed by selection and close breeding but not selfed	Earliness, size, quality
	do	Golden Gem	1928	Sunshine × Pickaninny	do	Extreme earliness and quality.
	Popcorn	Pinkie	1935	Black Beauty × Jap Hulless	Hybridization and selection	Novelty.

Texas	Sweet corn	Surcropper Sugar	1933	Country Gentleman × Surcropper.	Crossing and backcrossing repeatedly to field corn parent.	Earworm resistant, adapted to certain southern conditions.
	do	Honey June	1933	Country Gentleman × Mexican June.	do	Do.
Department (in cooperation with Indiana station.	do	Golden Cross Bantam	1932	Purdue 39 × Purdue 51	Hybridization	High yield, excellent quality, resistant to bacterial wilt, uniformity of type and maturity, high production of stover.
Department (in cooperation with Puerto Rico).	do	U. S. D. A. 34	1937	Native field corn and sweet mutation of native sweet corn.	Alternate generations of selfing and backcrossing on native field corn. The final crossing was a double-top cross between 2 second-generation inbred lines and 2 ear-to-row selections.	Resistant to corn stripe. Thick, tightly clasping husks. Vigorous plant, size similar to field corn. Large ears with kernels of unusual depth.
				MISCELLANEOUS CROPS		
Ohio	Beet	Ohio Canner	1932	Detroit Dark Red	Inbreeding and sib-mating	Dark color, round shape, absence of light rings.
Massachusetts	Carrot	Hutchinson	1923	Hutchinson	Mass selection	Long, smooth root; high yield.
California	Onion	California Early Red, U. C. No. 1.	1935	California Early Red	Inbreeding	Uniform size, shape, color, time of maturity, keeping quality.
	do	Australian Brown, U. C. No. 1.	1935	Australian Brown	Inbreeding, massing large numbers of similar unrelated lines.	Flesh color, scale color, keeping quality, fertility.
Colorado	do	Sweet Spanish, Colorado Station No. 6.	1936	Sweet Spanish	Inbreeding	Yield uniformity; better storage; improved color.
Texas	Peanut	McSpan	1925	Little Spanish	Pure-line selection	High yield, early maturity, high oil content.
Virginia (in cooperation with Department).	do	Experiment Station Jumbo.	1935	Jumbo	Selection	Very large pods and nuts; hard hulls.
Department	do	Spanish 18-38.	1925	Red Spanish.	do	Superior yielding capacity.
Connecticut (State)	Pepper	Windsor A	1936	California Wonder × Bountiful.	Hybridization	Early, productive; thick wall.
Louisiana	do	Baton Rouge Cayenne.	1934	Best local stocks of Red Cayenne.	Inbreeding	Size, uniformity, color, pungency and yield.
	do	C-2811 (not yet named)	1936	Baton Rouge Cayenne	Inbreeding and selection	Earliness, pungency; yield; resistant to defoliation by *Cercospora capsici*.
	do	Sport	1936	Native Sport × Honka (Japanese variety).	F_1 backcrossed to Honka to intensify red color.	Uniformity; productivity and superior color.
	do	T-10-1 (Tabasco)	1935	Best local stocks of Tabasco	Inbreeding	Uniformity; productivity; color; ease of harvesting.
	do	T-10-2 (Tabasco)	1935	do	do	Uniformity; fruit color and wall thickness; ease of harvesting.
Massachusetts	do	Waltham Beauty	1935	Unknown	Selection	Thick fruit; early; high yield.
New Mexico	do	Chile No. 9	1917	Mexican Chile	do	Improved adaptability, uniformity

[5] Released first to Illinois Canners Association in 1933 and to seedsmen in 1935.

TABLE 4.—*Improved varieties and strains of vegetable crops, peanuts, and sweet corn developed and released by State and Federal research agencies*—Con

MISCELLANEOUS CROPS—Continued

Station or U S Department of Agriculture	Crop	Variety name	Date introduced	Parents	Breeding method	Superior characters
Louisiana	Shallot	Unnamed	1936	2 local varieties	Crossing and selecting desirable F_1 plants	Resistance to pink root, fast growing, vigorous plants
	Sweetpotato	Porto Rico	1935	Porto Rico	Hill unit selection	Sprouts earlier, produces more plants per unit and 20 percent higher yield than parent stock
	do	Porto Blanco	1935	do	Mutation	White skin, white flesh, high yield high in starch ideally suited for starch manufacture, and for livestock feed
North Carolina	do	Porto Rico N C No 1	1928	do	Hill and tuber selection	High yield, smooth skin, uniform color uniform appearance
Department	do	Mameyita	1919	Unknown	Introduced from Puerto Rico	High quality, good keeper and yielder
	do	Japanese Yam	1930	do	Introduced from Japan	High starch content, resistant to *Fusarium batatatis* and *F hyperoxysporum*
	do	Oebi aboelan	1926	do	Introduced from Java	High quality and marked resistance to *F batatatis*
	do	Kloranda Dutch Yellow	1930	do	do	Do
Puerto Rico	Eggplant	Puerto Rican Beauty	1936	A 4 × University	Hybridization	Highly resistant to bacterial wilt

TABLE 5.—*Outstanding vegetable strains, varieties, and breeding lines of practical or theoretical interest that are in the cultures of State and Federal research agencies*

BEAN

Station or U.S Department of Agriculture	Crop or type	Variety name or no	Date obtained or started	How obtained	Parents	Characters of interest
Idaho	Canning	W-80	1934	Hybridization	Corbett Refugee × Stringless Refugee	Resistant to common bean mosaic, high productivity
	Garden	White Wax No 122	1935	do	Brittle Wax × White Refugee Wax	White seeded wax bean of Kidney Wax type
	do	Wax No 110	1935	do	Hybrid Wax U S No 536 × Corbett Refugee	A Refugee type wax bean resistant to common bean mosaic
	Semifield	Burtners Blight Proof	1934	Introduced by Mr Burtner, of Wasco County, Oreg	Not known	Resistant to curly top

Illinois	Lima	Henderson Bush 11 lines	(1)	Selection and crossing	Henderson Bush	Uniformity
	do	Wood s Prolific 4 lines	(1)	Selection	Wood s Prolific	Under test in 1936 for commercial value
	do	Baby Potato Lima, 6 lines	(1)	do	Henderson Bush	Henderson Bush vine and earliness, with small thick potato type beans crowded in pods Outyields Henderson
	do	Large Podded Henderson Bush 9 lines	( )	Cross between two selections	do	Large podded early, productive under Illinois conditions
Iowa	Green	Wholegreen		Hybridization	Burpee Stringless Green Pod × Refugee	Straight, stringless pods
			1930	do	Brittle Wax × unnamed	Attractive pod color
Minnesota	White pod	Fusduli	1932	Introduced	Unknown	Seed characters
New York (Cornell)			1915 to date	Numerous unnamed seedling	Hybrids of and selections from Robust, Wells Red Kidney, White Marrow Flat Marrow Scotia and White Imperial	Variously resistant to root rot, blight immune to mosaic and to specific strains of anthracnose
Department (in cooperation with Oregon)		About 100 lines	1928 to 1933	Hybridization	Resistant × susceptible varieties	Curly top resistance
		Corbett Refugee	1931	Selection from Sioux City Seed Co	Stringless Green Refugee	Mosaic resistant
Department (in cooperation with Colorado)		N 1092	1935	Hybridization	Brittle Wax × Corbett Refugee	Excellent wax bean type, good color and excellent pods
		N 675	1933	do	Pinto × Cranberry Striped Creaseback	Tolerant to bacterial blight
		Numerous other lines	Mostly since 1930	Hybridization and selection	American and foreign varieties	Disease resistance and adaptation possibilities

LEAFY CROPS

Arizona	Lettuce	Imperial No 152	In process	Selfing individual heads and roguing the increase	Imperial 152	Improved adaptation to Arizona conditions and conformity to varietal type
	do	Imperial No 615	do	do	Imperial 615	Do
Colorado	Lettuce head			Crossing	New York No 12 × Iceberg	Improvement in resistance to tipburn
Florida	Lettuce	1	1934	Selection	New York	Appears to show superior ability to develop hard head under certain growing conditions
	do	6	1934	do	do	Do
	do	15	1934	do	do	Do
	do	26	1934	do	do	Do
Hawaii	do	5 United States commercial varieties	1932	Introduced		Mignonette is good parent because of excellent heading under warm conditions Hybrids of California commercial varieties with Mignonette show promise

1 Started 1930 Best lines of 1936

Table 5.—*Outstanding vegetable strains, varieties, and breeding lines of practical or theoretical interest that are in the cultures of State and Federal research agencies*—Continued

LEAFY CROPS—Continued

Station or U S Department of Agriculture	Crop or type	Variety name or no	Date obtained or started	How obtained	Parents	Characters of interest
Minnesota	Brassica hybrids	1 35	1935	Hybridization	Brussels sprouts—cabbage hybrids	Gives promise of forming head and sprouts
	do	14-35	1935	do	do	Give promise of being an early type of brussels sprouts
	Crucifer hybrids	54 35 Fertile Hybrid	1930	do	Radish × cabbage	Generic hybrid of scientific interest May serve same purpose as rape
New York (Cornell)	Cabbage	Numerous strains	1919 to date		Homozygous for various factors and characters as purple, magenta sun color, and green, waxy dwarf types and others	Breeding stocks for practical or theoretical work
	do	Numerous lines	do		Intertype crosses of *Brassica oleracea* cabbage × cauliflower, brussels sprouts, kale, kohlrabi wild cabbage	For genetic study
	Celery			Hybridization	Golden Self Blanching × Utah	Self blanching, good quality, resistant to fusarium yellows
Department	Lettuce	4 lines	1929	do	Iceberg × Hanson	Heat resistant, reliable heading strains
	do	3 lines	1929	do	Mignonette × Hanson	High quality, early maturity
	do	7 lines	1929 and 1932	do	New York × Hanson	Solid, dark green, reliable heading types for eastern conditions
	do	MN 29-8-7	1929	do	Mignonette × New York	Tipburn and heat resistant
	do	P-1H-1190-3	1930	do	Two hybrid lines	Tipburn resistant
	do	IP-30-1 20	1930	do	Iceberg × Cos	Tipburn resistant, high edible quality
	do	MN-P-1193	1931	do	Two hybrid lines	Tipburn resistant, early maturity
	do	2 lines	1931	do	Imperial C × hybrid	Tipburn resistant
	do	2 lines C-NH-1 4	1931	do	do	Reliable heading
	do	6 lines	1931	do	Two hybrid lines	Tipburn resistant
	do	4 lines MN-NH-150	1932	do	do	Ability to head under adverse temperature conditions
	do	NT 12 1	1928	do	New York × Transport	Genetic material for chlorophyll deficiency
	do	BD-3 1	1928	do	California Cream Butter × Deacon	Genetic material for inheritance of Cos type
	(2)					
	do	M		Selection	Mignonette	Red *CCRRTT*
	do	B		do	California Cream Butter	Spotted *CCr'r'TT*
	do	I		do	Iceberg	Tinged *CCrrTT*
	do	H		do	Hanson	Green *CCRRtt*

	do	N		do	New York	Green $ccrrTT$
	do	T		do	Transport	Green $CCr'r'tt$
	do	C		do	Chavigne	Green $CCrrtt$
	do	NC		Hybridization	New York × Chavigne	Green $ccrrtt$
	do	MN		do	Mignonette × New York	Green $ccRRTT$
Department (in co-operation with Wisconsin)	Cabbage	77 lines homozygous for resistance to yellows	1930	Pure-line selection	Smith Pride variety	Useful for outcrossing to individuals selected for resistance
			PEA			
Maryland	Many lines		Mostly since 1928	Hybridization and pure lining	Commercial varieties	Wilt resistant
Department (in cooperation with California)	Progress type [3]	-	1932	Hybridization and selection	Laxton Progress × Giant Stride	Resistance to *Fusarium orthoceras pisi* Tolerance to unnamed Fusaria found at San Luis Obispo
	Hundredfold type [3]		1932	do	do	
	do	N762 and others	Mostly since 1932	Hybridization	do	Resistant to *Fusarium* tolerant to *Ascochyta*
	do	15 strains	do	do	Little Marvel × World Record F_4	Resistant to certain viruses Freezing types seed setting
	do	6 strains	do	do	Laxton Progress × Nain Mangetout F_4	Size of pod, hardiness
	do	132 strains	do	do	Laxton Progress × Giant Stride F_5–F_8	Resistant to fusarium wilts
	do	4 strains	do	do	Laxton Progress × World Record	Pod size seed setting
	do	30 strains	do	do	Laxton Progress × Kent Alderman	Pod size hardiness
	do	15 strains	do	do	Laxton Marvel × (Thomas Laxton × Phenomenon)	Resistant to certain viruses freezing types seed set resistant to fusarium wilts
	do		do	do	Austrian Winter × Alderman	Genetics and breeding for resistance to *Ascochyta* and *Mycosphaerella*
	do		do	do	Austrian Winter × Hundredfold	Do
	do		do	do	Austrian Winter × Perfection	Do
	do		do	do	Little Marvel × Progress F_1–F_3	Resistant to certain viruses
	Pisum elatius	2 strains	do	do		Not fully explored
	P jomardi	3 strains	do	do		Do
	Subspecies of *P sativum*	5 strains	do	do		Do
	Edible-podded	19 strains	do	do		Do
	Pure lines and varieties	300 strains	do	do		Do

[2] Homozygous genotypes for anthocyanin pigment in leaves of lettuce maintained at the Beltsville station
[3] It is planned to release these as soon as increased sufficiently

TABLE 5.—*Outstanding vegetable strains, varieties, and breeding lines of practical or theoretical interest that are in the cultures of State and Federal research agencies*—Continued

TOMATO, EGGPLANT AND PEPPER

Station or U. S. Department of Agriculture	Crop or type	Variety name or no.	Date obtained or started	How obtained	Parents	Characters of interest
California	Tomato	Many hybrids	1936	Hybridization	Red Currant × commercial varieties	Resistant to bacterial canker and spotted wilt
	do	Many varieties	1936	Inbreeding	Commercial stocks	Uniform type for variety
Georgia	Pepper	Pimiento	1928	Line selected	Perfection Pimiento	
	Tomato	Livingston Globe	1920	do	Livingston Globe	Resistant to wilt
	do	7-1-1	1926	Hybrid line selected for resistance to wilt and leaf diseases	Globe × Burpee	Resistant to wilt, heat, and drought
	do	22-3-1	1932	Above backcrossed to wilt resistant strain of Globe	(Globe × Burpee) × Globe	Do
	do	2-3-1-1	1932	Hybridization	Globe selection × Break o' Day	Resistant to wilt
Iowa	do	79		Crossing	Farliana × Best of All	Less cracking
Hawaii	do	Hawaii station hybrid	1918	Horticulture department	Obscure. Hybrid between a wild currant type and a commercial variety	Shows partial resistance to melon fly (*Bactrocera cucurbitae*) but has small size
	do	United States commercial varieties	1932–35	Introduced		
	do	2 local wild currant tomatoes				
Maryland	do	Strain of Red River No. 44-9	1930	Selection	Red River	Early; resistant to cracking
Minnesota	do	Various strains	1930–33	Breeding introduced	Numerous	Early; productive
Missouri	do	*Lycopersicon pimpinellifolium* × *L. esculentum* hybrids	1935	Hybridization	*Lycopersicon pimpinellifolium* × *L. esculentum*	Studies of fusarium wilt resistance and inheritance of resistance
New Hampshire	do	Bonny Best	------	Selection	Bonny Best	Strain adapted for forcing
	Eggplant	Unnamed	------	Dwarf Purple × Black Beauty	Hybridization	Earliness; adaptability to Northern States
New Jersey	Tomato [4]	Marglobe × J. T. D. crosses	------	Crossing and selection	Marglobe × J. T. D.	Undergoing selection for improved yield, fruit shape, color, and general high quality
	do	Break o' Day × Oxheart crosses		do	Break o' Day × Oxheart	Do
	do	Marglobe × Earliana crosses		do	Marglobe × Earliana	Being selected for larger, smoother, high-quality, early market tomato

Tennessee	do	Usual commercial varieties.				
Texas	do	B-1	1935	Hybridization	Large Cherry × Bonny Best.	Sets fruit under unfavorable conditions; prolific.
	do	377	1935	do	Gulf State Market × Cherry.	Sets fruit under unfavorable conditions; prolific; free from "puff."
Department.	do	50 Marglobe lines	1932	Inbreeding	Marglobe	Wilt-resistance studies.
	do	50 lines	1925–35	Hybridization	Marglobe and other commercial sorts.	Being tested prior to release of best; wilt and nailhead resistant.
	do	125 varieties	1932	Inbreeding	European varieties	For disease-resistance and inheritance work.
	do	130 varieties	1932	do	American varieties	Do.
	do	100 varieties	1935–36	Introduction	Australian, South American, and Asiatic sources.	Do.
	do	Numerous lines	1935	Hybridization and backcrossing.	*Lycopersicon pimpinellifolium* × *L. esculentum* and reciprocals.	Do.
Wyoming	do	Denmark	1932	Denmark		Desirable type and fruiting habit.
	do	Bonny Best	1930	U. S. Department of Agriculture.		High quality.
	do	Bison	1932	North Dakota Agricultural College.		Early.
	do	Yellow Pear	1930	U. S. Department of Agriculture.		Do.
	do	Currant	1930	do		Do.
Puerto Rico.	Eggplant	A-4	1930	Hybridization	Black Beauty × Fajardo	Resistant to bacterial wilt.

CUCURBITS

Arizona	Cantaloup	McDaniels Nugget	In process	Selfing individual plants and rigidly roguing each strain.	McDaniels Nugget	Uniform size, globe shape, deep flesh, salmon color, deep net, high sugar.
	do	Superfecto	do	do	Superfecto	Do.
California	Muskmelon	Hale Best	1926–36	Inbreeding; 10–15 inbred lines being carried along.	Commercial stocks	Uniformity of plant and fruit characters.
	do	Salmon Tint	1926–36	do	do	Do.
	do	Honey Dew	1926–36	do	do	Do.
	do	Honey Ball	1926–36	do	do	Do.
	do	Persian	1926–36	do	do	Do.
	do	Casaba	1926–36	do	do	Do.
	do	Many minor horticultural varieties and subspecies.	1926–36	One or more inbred lines		
	Squash	White Bush Scallop	1930–36	10–15 inbred lines of each	Commercial stocks	Uniformity of fruit and plant characters.
	do	Giant Summer Crookneck.	1930–36	do	do	Do.
	do	Giant Summer Straightneck.	1930–36	do	do	Do.

[4]Other crosses: Marglobe × Stone, Argentina × Gulf State Market, Shanghai × Marvel, Cooper × J. T. D., Peiping × J. T. D , Pritchard × J. T. D., and others.

Table 5.—*Outstanding vegetable strains, varieties, and breeding lines of practical or theoretical interest that are in the cultures of State and Federal research agencies*—Continued

CUCURBITS—Continued

Station or U. S. Department of Agriculture	Crop or type	Variety name or no.	Date obtained or started	How obtained	Parents	Characters of interest
California	Squash	Grey Zucchine	1930–36	10–15 inbred lines of each	Commercial stocks	Uniformity of fruit and plant characters
	Watermelon	California Klondike No. 1	1933	Inbreeding	do	Uniform fruit type, high sugar, prolific
	do	California Klondike No. 3	1933	do	do	Do
	do	California Klondike No. 8	1933	do	do	Uniform fruit type, tough rind
	do	Striped Klondike No. 11	1936	do	do	Uniform fruit type, high sugar
	do	Thurmond Grey No. 46	1936	do	do	Uniform fruit type for variety
	do	Golden Honey No. 28	1936	do	do	Do
	do	Baby Delight No. 32	1936	do	do	Do
	do	Winter Queen No. 213	1936	do	do	Do
	do	Peerless No. 247	1936	do	do	Do
	do	Angelino No. 3	1936	do	do	Do
	do	Chilean No. 7	1936	do	do	Do
	do	Snowball No. 12	1936	do	do	Do
	do	Stone Mountain No. 44	1936	do	do	Do
	do	Long Mountain No. 216	1936	do	do	Do
	do	Northern Sweet No. 251	1936	do	do	Do
	do	Sun Moon Stars No. 265	1936	do	do	Do
	do	Grey Monarch No. 260	1936	do	do	Do
	do	Iowa Belle No. 542	1936	Hybridization	Unknown	Uniform fruit type for variety, resistant to wilt
	do	Pride of Muscatine No. 136	1936	Inbreeding		Do
	do	Hybrid No. 7	1936	Hybridization	Klondike × Iowa Belle	Klondike type, resistant to wilt
	do	Hybrid No. 19	1936	do	do	Kleckley type, resistant to wilt
	do	Hybrid No. 16	1936	Inbreeding		Klondike type, resistant to wilt
Florida	Cantaloup	Rocky Dew	1935	From Kilgore Seed Co.	Rocky Dew	Resistant to mildew and certain leaf spots
	Squash	African	1933	Plant Exploration and Introduction, U. S. Department of Agriculture	African squash	Superior eating quality and yielding ability, considerable resistance to stem borer
	Watermelon	Iowa Belle	1931	Introduced from Iowa		Shows some resistance to wilt under Florida conditions
	do	Iowa King	1931	do		Do
Iowa	Squash	Improved Table Queen		Inbreeding	Isolation of high yielding inbred lines	Increased uniformity and yield and freedom from mixtures

Louisiana	do	Sugar Bowl		Crossing and backcrossing	Scalloped White Bush × Des Moines.	Very uniform; deep teacup shape; white color; very fleshy; sweet; high quality.
Maine	Cucumber	Line 155	1932	Selfing	Windermoor Wonder	Resistant to scab (*Cladosporium cucumerinum*).
	do	Line 128	1932	do	Longfellow	Do.
Massachusetts	Squash	Blue Hubbard No. 1		Selfed pure line	Commercial Blue Hubbard.	Uniform fruit; high yield; good color; strain lacks roughness desired by growers.
Michigan	Muskmelon	Honey Rock inbreds	1935	Inbreeding	Honey Rock	Some lines for hard shell and ropy net.
	do	$3=S_5$; $2=S_6$		do		Some lines for thick flesh and high total solids.
	do	1730 F_3	1935	Hybridization	Hale Best × Honey Rock	Thick flesh of Hales and shell and net of Honey Rock (not fixed as yet).
	do	1731 F_2	1935	do	(Hale Best × Honey Rock) × Honey Rock.	More characters of recurrent parent.
	do	1739 F_5	1935	do	Honey Dew × Emerald Gem.	Orange flesh of Emerald Gem; shell of Honey Dew.
	do	4 F_3 lines	1937	do	Honey Dew × Champlain on Hearts of Gold.	Early maturing; green flesh. Honey Dew.
Minnesota	Cucumber	Numerous strains	1914-36	Introduction; selection. inbreeding. hybridization.	Many varieties	Pure lines for several genetic characters.
	Muskmelon	do	1932	Selection	Golden Osage	Resistant to fusarium wilt.
	Watermelon	do	1931	Hybridization	Arikara, Northern Sweet, Fordhook, Angelino, Winter Queen.	Early; seed color; quality.
	Squash	do	1920 36	Introduction; selection; inbreeding, hybridization	Many varieties	Pure lines for several genetic characters.
New Hampshire	Cucumber	Granite State	25-30 years ago	Hybridization	English × White Spine	Excellent forcing cucumber; thirfty grower; prolific.
New York (Geneva)	Squash	*Cucurbita moschata* × *pepo* 31.	1933	do	Japanese Pie × Early Yellow Bush Scallop.	Potential disease resistance.
	do	*Cucurbita moschata* × *pepo* 32.	1933	do	Japanese Pie × Mammoth Yellow Bush Scallop.	Do.
	do	*Cucurbita pepo* × *moschata* 43.	1933	do	Giant Summer Crookneck × Japanese Pie.	Do.
	do	*Cucurbita moschata* × *maxima* 52.	1933	do	Quaker Pie × Banana	Do.
	do	*Cucurbita moschata* × *pepo* 64.	1933	do	Japanese Pie × Delicata	Do.
	do	*Cucurbita pepo* × *moschata* 70.	1934	do	Bohemian (=Delicata) × Japanese Pie.	Do.
Department (in cooperation with California).	Muskmelon	Numerous lines		do	American and oriental sorts.	Powdery mildew resistance.

TABLE 5.—*Outstanding vegetable strains, varieties, and breeding lines of practical or theoretical interest that are in the cultures of State and Federal research agencies*—Continued

CUCURBITS—Continued

Station or U S Department of Agriculture	Crop or type	Variety name or no	Date obtained or started	How obtained	Parents	Characters of interest
Department at Beltsville, Md	Cucumber	40 lines	Mostly since 1930	Inbreeding	Japanese and Chinese varieties	Some resistance to mosaic
	do	50 lines		Hybridization	American × Japanese or Chinese varieties and reciprocals	Do
	do	10 lines		Inbreeding	American and oriental varieties	Some resistance to bacterial wilt
	do	20 lines		Hybridization	do	Do
	do	6 lines		Inbreeding	Chinese and Indian varieties	Some resistance to downy mildew
	do	5 lines		Hybridization	Chinese × American varieties	Do
Department at Corvallis, Oreg	Squash	Several lines	1932	Inbreeding	Marblehead	Uniform productive, resistant to curly top
	do	do	1933	Hybridization	Marblehead × Beau Dessert	High quality adapted to Northwest
	do	do	1932	Inbreeding	Varieties of *Cucurbita pepo*	Potential disease resistance
Department at Cheyenne, Wyo	Muskmelon	Griffin	1934	Canada		Early maturity
	do	John the Gardener	1934	Wyoming gardener		Early maturity and quality
	do	Vine Peach	1935	Commercial		Tartness of flavor early maturity
	do	Hale Best	1935	do		High quality
	Squash and pumpkin	New England Pie	1930	do		Early, and good quality
	do	Cocozelle	1930	do		Bush habit of growth
	do	Giant Summer Crookneck	1930	do		Bush habit of growth early,
Puerto Rico	Cucumber	Chinese Long	1933	Introduction		Resistant to downy mildew
	do	35-2 8-3 2	1935	Hybridization	Chinese Long × Early Black Diamond	Do

SWEET CORN

California	Sweet corn	Papago	1934	Associated Seed Growers, Inc.	Commercial stocks	Earworm resistant.
	do	Honey June	1934	Texas Agricultural Experiment Station.		Earworm and heat resistant.
	do	California No. 1	1935	Hybridization	(Honey June × Oregon Evergreen) × Honey June.	Earworm resistant.
	do	California No. 2	1935	do	(Honey June × Oregon Evergreen) × Oregon Evergreen.	Do.
	do	California No. 3	1935	do	(Honey June × Golden Bantam) × Honey June	Do.
	do	Surcropper Sugar	1934	Texas Agricultural Experiment Station		Do.
	do	Florida 191	1934	Florida Agricultural Experiment Station.		Do.
	do	Oregon Evergreen	1934	F. Lagomarsino.	Commercial stock	Do.
	Dent corn	Mexican June	1934	Aggeler & Musser	do	Earworm and heat resistant.
	do	King Philip	1935	F. Lagomarsino	do	Earworm resistant; yellow kernels.
	do	Davis Prolific	1935	Reuter Seed Co.	do	Earworm resistant.
	do	Tuxpan	1935	Texas Agricultural Experiment Station.		Do.
Connecticut (State)	Sweet corn	Connecticut 2	1933	Inbreeding	Whipple	Dark green foliage, vigorous plant, narrow kernel.
	do	Connecticut 6	1933	do	do	Light green foliage, resistant to bacterial wilt, broad kernel.
	do	Connecticut 7	1933	do	do	Narrow kernel, good plant and ear.
	do	Connecticut 13	1935	do	Golden Early Market	Very resistant to bacterial wilt. Golden Early type of ear.
	do	Connecticut 78	1926	do	Red leaves (probably from Crosby).	Good quality.
	do	Connecticut 77	1926	do	Stowell Evergreen.	Large ear, good quality, pearly white.
	do	P 39			(?)	Good quality; adaptability; resistant.
	do	P 51			Golden Bantam	Good quality; 8-rowed ear.
Florida	do	Sweet Snowflake	1934	Recurrent backcrossing	Snowflake, Long Island Beauty.	Husk protection, southern type.
	do	Alachua Sweet	1935	do	White Dent, Long Island Beauty.	Do.
	do	Sweet Dubose	1935	do	Dubose, Long Island Beauty.	Do.
	do	Sweet Tuxpan	1935	do	Tuxpan, Florida 191	Husk protection; adapted to Everglades.
	do	Sweet Oklahoma Silvermine.	1935	do	Oklahoma Silvermine, Suwannee Sugar.	Husk protection, southern type.
	do	Sweet Trucker Favorite	1935	do	Trucker Favorite, Suwannee Sugar.	Husk protection, southern type; earliness.

TABLE 5.—*Outstanding vegetable strains, varieties, and breeding lines of practical or theoretical interest that are in the cultures of State and Federal research agencies*—Continued

SWEET CORN—Continued

Station or U. S. Department of Agriculture	Crop or type	Variety name or no.	Date obtained or started	How obtained	Parents	Characters of interest
Florida	Sweet corn	Florida King Bantam	1935	Recurrent backcrossing	Hickory King, Cuban Flint, Suwannee Sugar.	Husk protection, southern type, Golden Bantam ear type, tender and very good quality.
Illinois	do	22-507-806-4-104-203	( )		Iowa State College No. 15 Evergreen × Yellow Dent.	(6).
	do	81-521-818-108-7-106-206 and 207.	(5)		Open-pollinated Bantam Evergreen.	
	do	84-528-110-9-108-209 and 210.	(5)		Open-pollinated Whipple's Early Yellow.	
	do	192-537-832-10-109-211 and 212.	(5)		Purdue 1339-1-1-2-1-1-1	
	do	202-544-838-113-12-111-214 and 215.	(5)		Purdue No. 25	
	do	203-545-839-13-112-216 and 217.	(5)		Purdue No. 29	
	do	204-546-840-114-14-113-218.	(5)		Purdue No. 34	
	do	206-548-842-115-15-114-219.	(5)		Purdue No. 38	
	do	212-554-848-16-115-220 and 221.	(5)		Purdue No. 1313 × 1324	
	do	5004-1A-1-1-19-4-121-226	(5)		Illinois No. 14 × Yellow sweet.	
	do	5020-1-1-1-129-234	(5)		Wisconsin (589 31 × 3) × Purdue (1339 × 1313).	
	do	5030-1-1-1-132-237	(5)		Open-pollinated Bantam Evergreen × (Purdue 1313 × 1319).	
	do	5041-1-1-1-134-239	(5)		Purdue 1339-1-2-3-1-1-1 × Iowa State College S 760-1.	
	do	5043-1-1-1-136-242	(5)		Purdue (1308 × 1313) × Purdue (1313 × 1335).	
	do	5044-1-1-1-137-243	(5)		Purdue (1308 × 1335) × Wisconsin 589 31 × 3.	
	do	5044-1-1-1-138-244	(5)		Purdue (1308 × 1335) × Wisconsin 589 31 × 3.	
	do	5050-1-1-1-141-247 and 248.	(5)		Purdue (1313 × 1324) × Purdue (1339 × 1313).	

	do	5051 1 1 1 249	( )		Purdue (1313 × 1324) × Purdue (1351 × 1313)	
	do	5055-1 2 1 252 and 253	(		Inbred from Purdue 21 × inbred from Purdue 29	
	do	5059-1 2 1 255	(		Inbred from Purdue (1308 × 1335) × inbred from Purdue 34	
	do	5061 1 1 1 257			Inbred from [Wisconsin (5939 × 4) × Purdue (1339 × 1313)] × inbred from Purdue 36	
	do	5068-2 1 2 260			Illinois Narrow Grain Evergreen × yellow sweet	
	do	5068-4-1-1 262			do	
	do	5068-4-1-2-263 264 and 265			do	
	do	5068-4-1-3-266 and 267			do	
	do	5068-5-1-2-272 and 273			do	
	do	5068 5-1-4-275			do	
	do	5068-8-1 1 276			do	
	do	5068-8-1 3-278			do	
	do	9 hybrids	1935	Hybridization	Narrow Grain Evergreen × Country Gentleman	Superior yield
Indiana (in cooperation with Department)	do	G B 14	1921	Pure line selection	Golden Rod	Excellent pollinator few suckers good quality
	do	G B 51B	1922	do	Golden Bantam	Carries factor for high yield, tall, slender plant Good pollen parent
	do	C G 22	1921 [7]	do	Country Gentleman	Resistant to kernel infection Produces an early top cross with open pollinated strains Two ear type
	do	C G 34	1931	do	do	Carries factor for kernel depth
	do	C G 6355	1928	do	do	Stiff stalk root rot resistant
	do	S F 4-6	1921	do	Stowell Evergreen	Productive good seed quality
	do	S F V4	1928	do	do	Productive root rot resistant
	do	N G 119	1921	do	Narrow Grain Evergreen	Deep, narrow kernel erect resistant to ear rots
	do	N G 1014 2 5	1921	do	do	Good root system, slender ear
Iowa	do	Iogold 18 39		Crossing of inbred lines	Sunshine inbreds	Increased yield and uniformity
	do	Iogent 16 45 Iogent 90 45		do	Country Gentleman inbreds	Do
	do	Iogreen 123 91 Iogreen 11 63		do	Narrow Grain Evergreen inbreds	Do

[5] Work started in 1929 and the lines listed are those showing merit as of 1935

[6] These lines are all inbreds the number of generations inbred being indicated by the number of integers in the pedigree A great many additional inbreds are being maintained (142 inbred lines in all) but only those showing distinct merit are listed The object is to secure single crosses able to withstand the heat and drought of central Illinois and to show a high degree of resistance to bacterial wilt Purdue Golden Cross Bantam is not sufficiently resistant to wilt for the purpose All the lines listed show promise They range all the way from extremely early 8 row to late maturing 18 row types

[7] First year of inbreeding

TABLE 5.—*Outstanding vegetable strains, varieties, and breeding lines of practical or theoretical interest that are in the cultures of State and Federal research agencies*—Continued.

SWEET CORN—Continued

Station or U. S. Department of Agriculture	Crop or type	Variety name or no.	Date obtained or started	How obtained	Parents	Characters of interest
Maryland	Sweet corn	About 50 inbreds	Mostly since 1930.	Hybridizing sweet × dent corn followed by inbreeding. Own production.	Commercial varieties	Yield and adaptability.
	do	Many inbreds		Commercial and research agencies.		For comparison.
New York (State)	do	G5.	1927	Inbreeding	Golden Bantam	High quality; potent hybridizer.
Pennsylvania	do	Purdue 39	1936	From Glenn Smith, Lafayette, Ind.		
	do	Purdue 51	1936	do		
	do	Purdue 13391-8-1	1936	do		
	do	Purdue 1351-3-1-1-2.	1936	do		
	do	Purdue 3-1-3-2	1936	do		
	do	Purdue 1308	1936	do		
	do	Purdue 8482	1936	do		
	do	Purdue 14-1-2-6	1936	do		

MISCELLANEOUS CROPS

Station or U. S. Department of Agriculture	Crop or type	Variety name or no.	Date obtained or started	How obtained	Parents	Characters of interest
Minnesota	Asparagus	375 different plants, nos. 2-1 to 9-43.	1932	Selection	Washington	Production and breeding records known.
Department	Beet	Several lines	Mostly since 1930.	Highly uniform inbreds from commercial varieties.	Commercial varieties	Some commercial possibilities; others of genetic interest only.
Minnesota	Carrot	36-34, 37-34	1934	Selection and inbreeding	Chantenay	Uniform.
California	Garlic	Early or Mexican		Selection	Commercial stocks	
	do	Late or Italian		do	do	
	do	Many introductions			Through Plant Exploration and Introduction.	
Louisiana	Okra [a]					
California	Onion	Stockton Yellow Globe 36-40.		Selfed one generation	Stockton Yellow Globe (commercial stock).	Uniform; nonbolting.
	do	White Persian	1929	Plant Exploration and Introduction.	P. E. I. No. 86279	Thrips resistant.
	do	Stockton Yellow 21-1-3-4-S_4.		Inbreeding	Stockton Yellow (commercial).	Nonbolting.

	do	Italian Red 13–53		Selection	Italian Red (commercial)	Male sterile mildew resistant
	do	Lord Howe Island		Australia	Lord Howe Island	Deep red, early
	do	Australian Brown No 17		Inbreeding	Australian Brown	Resistant to pink root
	do	Sweet Spanish No 35		do	Sweet Spanish	Do
	do	Nebuka		Japan	Nebuka selection	Do
Louisiana	do	Creole		Inbreeding and selection followed by intercrossing similar lines and mass open pollination of similar lines (Stocks maintained at Louisiana)	Best local stocks	Excellent keeping quality, high total solids Very strong flavor, desired by certain markets and processors Adaptable to short-day growing conditions
Texas	do	White Persian	1935	California station		Disease resistant
	do	Crystal Wax	1935	Selection	Individual plants	Deep nonsplitting
Georgia	Peanut	Improved White Spanish	1931	Tom Huston Peanut Co		Small, uniform seed of high quality
	do	Pearl	1931	do		White seed coat poor quality
	do	Carolina Runner	1931	do		Resistant to disease high yield
	do	Virginia Runner	1931	do		Resistant to disease, large seed
	do	Virginia Bunch	1931	do		Bunch, large seed
	do	Jumbo	1931	do		Large seed fairly resistant to disease
	do	Tennessee Red	1931	do		Bunch, large pods suitable for roasting
	do	Basse	1931	do		Resistant to disease, well filled
	do	West African	1931	do		Resistant to disease
	do	Philippine White	1931	do		Resistant to disease, white seed
	do	Kimorales	1931	do		Bunch, fairly resistant to disease
	do	Java P I	1931	do		Bunch said to be resistant to bacterial wilt
	do	H13–36–66	1934	Selected hybrid	Pearl × Carolina Runner	Resistant to disease fine hay
	do	H19–54 13–3	1935	do	Improved White Spanish × Carolina Runner	Do
	do	H21 39–39	1934	do	Improved White Spanish × Virginia Runner	Do
Virginia (in cooperation with Department)	do	15 selections from Virginia Runner	1935	Selection	Virginia Runner	Large pods hard seed hulls and superior yields
Department (in cooperation with Virginia and South Carolina)	Peanut	About 250 varieties and introduction	Mostly since 1930	Mostly by introduction	Mostly through Plant Exploration and Introduction	Largely unexplored
Minnesota	Rhubarb	Various strains	1932 36	Inbreeding selection introduction	Several varieties	Improved color and quality
Hawaii	Sweetpotato	Black Spanish	1934	Introduced		
	do	Red Jersey	1922	do		
	do	Dixie Yam	1922	do		
	do	Jewel Yam	1922	do		
	do	Priestly	1934	do		
	do	Creola	1922	do		
	do	Pohrico	1934	do		

[a] Pure lines of the leading varieties are being maintained at the Louisiana station
[b] These selections have been placed in the hands of a selected group of growers for multiplication and distribution

TABLE 5.—*Outstanding vegetable strains, varieties, and breeding lines of practical or theoretical interest that are in the cultures of State and Federal research agencies*—Continued

MISCELLANEOUS CROPS—Continued

Station or U S Department of Agriculture	Crop or type	Variety name or no	Date obtained or started	How obtained	Parents	Characters of interest
Hawaii	Sweetpotato	Japanese Brown	1917–22	Introduced		
	do	Nancy Hall	1934	do		
	do	Vineless Yam	1934	do		
	do	Merced	1934	do		
	do	Madeira	1917	do		
	do	40 Hawaiian varieties	1917–35	Collected from various islands		
	do	20 hybrids	1926–29	Hand crosses of known varieties		
	do	40 open pollinated seedlings	1934	Seed collected in field open pollinated		Selection for eating quality is most important object
Maryland	do	Menes Moeder	1923	Introduction	Introduced from Java	High quality and marked resistance to *Fusarium batatatis*
Department	do	do	1923	do	do	High starch content Resistant to *Fusarium batatatis* and *F. hyper-oxysporum*
	do	254	1923	do	Big Wig × (?)	
	do	291	1923	do	do	
	do	About 25 varieties	Since 1919	From growers in United States	Unknown	Of commercial interest in past or at present
	do	About 30 numbers	Since 1919	Foreign introductions	do	Of potential commercial and breeding value Many are resistant to *Fusarium*
	do	About 100 seedlings	Since 193	Open pollinated seed	Female parent known	Do

Table 6.—*Recent vegetable breeding activities of State and Federal agencies in the United States*

[Parentheses enclose names of investigators no longer connected with the institution]

State or department and crop	Nature of studies	Personnel
Alabama:		
Vegetables	Searching the State for superior strains or plants	C. L. Isbell.
Arizona:		
Lettuce and cantaloup.	Selection within commercial varieties for local adaptation.	W. E. Bryan, M. F. Wharton.
California:		
Asparagus	Inheritance of spear size, shape, head tightness, toughness, node size.	(H. A. Jones, G. C. Hanna.)
Cantaloup (part in cooperation with Department).	Inheritance of fruit size and qualitative characters, resistance to powdery mildew. Effect of inbreeding.	(J. T. Rosa,[1] G. W. Scott), I. C. Jagger,[2] T. W. Whitaker.[2]
Celery	Inheritance of pithiness and bolting	(S. L. Emsweller.)
Onion	Inheritance of color of flesh, scale, foliage, seed; size of seed; bolting; sterility. Cytology of *Allium* species hybrids. Resistance to thrips.	(H. A. Jones, S. L. Emsweller)
Peas	(See Department cooperation with California)	
Squash (*Cucurbita pepo*).	Inheritance of fruit and plant characters and fruit size. Effect of inbreeding.	(G. W. Scott.)
Spinach	Inheritance of resistance to mosaic	Do.
Sweet corn	Determination of factors governing earworm resistance; nature of factor interaction in hybrid vigor by crossing inbred lines.	(C. F. Poole.)
Tomato	Inheritance of fruit size; resistance to spotted wilt and bacterial canker.	(O. H. Pearson), D. R. Porter.
Watermelon	Inheritance of color of flesh, rind, seed coat; sugar content, rind toughness; size of seed; resistance to wilt.	(J T. Rosa,[1] G.W. Scott), D. R. Porter (C. F. Poole).
Colorado:		
Bean (snap)	Breeding for mosaic resistance and adaptability to canning in Colorado.	A. M. Binkley.
Lettuce	Breeding for tipburn resistance by intervarietal crossing and selection.	Do
Onion	Inbreeding and selection in Sweet Spanish for improved market type and adaptability to Colorado.	Do
Connecticut:		
Bean (lima)	Selection for high yield	D. F. Jones, W. T. Singleton, L. C. Curtis.
Pepper	Inheritance of seedless character	Do.
Squash	Nature of hybrid vigor by crossing inbred lines.	Do.
Sweet corn	Development of early, disease-resistant, high quality, productive new varieties and hybrids for canning and market through use of inbreeding, hybridization, and production of "synthetic varieties." Inheritance of several seed, seedling, and plant characters, and study of zygotic and gametic lethals. Studies of hybrid vigor.	Do.
Delaware:		
Cabbage	Inheritance of qualitative characters	L. R. Detjen, E. W. Greve.
Florida:		
Sweet corn	Developing earworm-resistant sweet corn of good quality adapted to Florida by intervarietal crosses, backcrosses, and selection.	F. H. Hull, W. A. Carver.
Tomato	(See Department cooperation with Florida.)	
Watermelon	Selection for wilt resistance	M. N. Walker.
Georgia:		
Peanut	Inheritance of color of leaf and seed coat; growth habit; size and shape of seed and pods; size and shape of leaflets; resistance to cercospora leaf spots, *Sclerotium rolfsii* and physiological seed spot. Hybrid vigor.	N. C. Woodroof.
Tomato	Intervarietal crosses for wilt resistance and adaptation to Georgia conditions.	H. L. Cochran.
Hawaii:		
Lettuce	Hybridization and selection to obtain varieties that will head well at low altitude in the subtropics.	(C. P. Wilsie), J. H. Beaumont, M. Takahashi.
Sweetpotato	Controlled hybridization, selection, and use of open-pollinated seed to obtain high quality, yield, and if possible resistance to weevil.	Do.
Tomato	Intervarietal and species crosses and selection to obtain resistance to melon fly. Resistance to late blight and mosaic being sought.	Do.
Idaho:		
Bean	Development of improved disease-resistant varieties by intervarietal crossing and by pure-line selection. Inheritance of resistance to common bean mosaic.	W. H. Pierce, Leif Verner, G. W. Woodbury.

[1] Deceased.
[2] Of U. S. Department of Agriculture.

TABLE 6.—*Recent vegetable breeding activities of State and Federal agencies in the United States*—Continued

State or department and crop	Nature of studies	Personnel
Illinois:		
Bean (lima)	Intervarietal crosses and pure-line selection for improved yield and adaptability to Illinois conditions.	W. A. Huelson.
Sweet corn	Inheritance of rowing, nature of hybrid vigor in crosses of inbred lines. Production of high yield and quality sweet corn for Corn Belt conditions.	Do.
Tomato	Intervarietal crosses and selection for wilt resistance in field and greenhouse types and adaptation to high-nitrogen prairie soils.	Do.
Indiana:		
Tomato	Selection for wilt resistance and improved adaptability to Indiana conditions.	E. C. Stair, (J. H. MacGillivray).
Iowa:		
Bean (snap)	Intervarietal crossing and selection for high-quality beans adapted to Iowa.	A. T. Erwin, E. S. Haber.
Tomato	Intervarietal crossing and selection for high-quality tomatoes adapted to Iowa.	Do.
	Nature of inheritance of specific qualitative factors, determination of linkage relations, inducing and studying inheritance of new variants, study of polyploid forms and cytology thereof.	E. W. Lindstrom
Sweet corn	Improving yield and uniformity through crossing of inbreds developed from commercial varieties. Inheritance of resistance to drought and bacterial wilt.	A. T. Erwin, E. S. Haber.
Louisiana:		
Collard, carrot, okra, pepper.	Inbreeding and selection to obtain strains of superior market value and productivity adapted to Louisiana conditions.	J. C. Miller.
Cabbage, onion	Crossing of inbred lines to attain objectives stated above.	Do.
Shallot, squash, tomato.	Crossing and backcrossing commercial varieties to attain objectives stated above.	Do.
Sweetpotato	Hill unit selection and isolation of mutants to improve stocks and obtain new sorts of specific value as for starch manufacture.	
Maine:		
Bean	Selection, crossing, and backcrossing to improve Yellow Eye type; development of blight- and anthracnose-resistant sorts. Inheritance of eye pattern, color, vine characters, seed size, and linkage relations.	(F. M. Surface, K. Sax), H. C. McPhee, (F. V. Owen), I. M. Burgess, (C. R. Burnham), R. M. Bailey.
Cucumber	Inbreeding and selection for resistance to *Cladosporium cucumerinum*.	I. M. Burgess, R. M. Bailey
Tomato	Selection for earliness and resistance to cracking	R. M. Bailey.
Maryland:		
Cantaloup, sweetpotato.	Selection for quality, yield, and adaptation	T. H. White.
Pea	Selection for resistance to wilt	C. E. Temple.
Spinach	Mass selection for increased winter hardiness	(F. W. Geise, H. B. Cordner)
Sweet corn	Study of natural selection in successive generations of sweet × dent corn cross. Development of varieties and hybrid sweet corns from inbreds from sweet × dent crosses. Studies of hybridization technique.	W. B. Kemp, R. G. Rothgeb (A. Stabler).
Tomato	Hybridization and selection for quality, yield, and adaptation.	T. H. White, J. B. S. Norton.
	Early work on selection for disease resistance.	
Massachusetts:		
Asparagus	Selection and crossing selected plants to study transmission of yielding ability.	Robert E. Young.
Celery	Development of superior strains of Pascal through inbred selections.	Do.
Lettuce (cooperation with Department).	Hybridization and selection to obtain crisp heading varieties and greenhouse types for Massachusetts.	Do
Squash	Development of superior strain of Warted Blue Hubbard by inbred selections.	Do.
Tomato	Hybridizing *Lycopersicon pimpinellifolium* and *L esculentum* to obtain leaf mold resistance.	F. F. Guba.
Michigan:		
Beans	Crossing and backcrossing varieties to obtain higher quality, darker green, mosaic resistance, and better pod-setting in canning sorts.	C. H. Mahoney, H. L. Seaton, Ray Nelson, Miriam Strong.
Brussels sprouts	Inbred selections (greenhouse bud pollination) to develop strains for upland and for muck soils.	Do.

TABLE 6.—*Recent vegetable breeding activities of State and Federal agencies in the United States*—Continued

State or department and crop	Nature of studies	Personnel
Michigan—Continued.		
Celery	Inheritance of resistance to yellows	C. H. Mohony, H. L. Seaton, Ray Nelson, Miriam Strong.
Cucumber	Inbred selections for greater fruit length in National Pickle.	Do.
Muskmelon	Inheritance of netting and sterility. Honey Rock inbred selections for hard rind and ropy net; for thick flesh and high solids. Varietal crosses and backcrosses involving Hale Best, Honey Dew, Honey Rock, Emerald Gem, Champlain, and Hearts of Gold for improved quality, appearance, and adaptability of specific new combinations of characters.	Do.
Radish	Root selection for short top, uniformity, shape, and color in Scarlet Globe.	Do.
Sweet corn	Inbreeding, hybridization, and selection for resistance to European corn borer, tolerance to bacterial wilt, and high canning quality. Development of desirable inbred pollen parents.	Do.
Minnesota:		
Asparagus	Selection within Washington strains to improve yield and study transmission of yielding ability.	(R. Wellington, J. W. Bushnell, W. T. Tapley), F. A. Krantz, T. M. Currence, A. E. Hutchins, assisted by J. G. Leach, T. M. McCall, T. S. Weir, M. J. Thompson.
Bean	Inheritance of several qualitative and quantitative characters.	Do.
Brassica spp.	Genetic and cytological study of cabbage × radish and Brussels sprouts × cabbage hybrids.	Do.
Carrots	Selection of superior strains through inbreeding	Do.
Cucumber	Inheritance of a number of qualitative and quantitative characters including plant height, determinate growth, and study of shape correlations.	Do.
Cucurbits, other (muskmelon, squash, watermelon).	Varietal crosses and selection to develop fusarium wilt resistance. Inheritance of qualitative factors in squash.	Do.
Eggplant	Studies similar to those on cucumber	Do.
Pepper	Inheritance of several qualitative and quantitative characters, studies of shape correlations.	Do.
Rhubarb	Inbreeding, selection, hybridization for improving petiole color and quality.	Do.
Tomato	Inheritance of growth habit, time of ripening, fruit size. Effect of polyploidy on economic characters. Study of certain linkages.	Do.
New Hampshire:		
Eggplant	Varietal crosses and selection to obtain earlier sorts adapted to Northern States.	J. R. Hepler, G. F. Potter.
Tomato	Selection of locally adapted forcing strains. Study of hybrid vigor in intervarietal crosses.	Do.
New Jersey:		
Tomato	Varietal crosses, backcrosses and selection for improving yield, color, and wilt resistance of canning types.	L. G. Schermerhorn, C. M. Haensler.
New Mexico:		
Onion	Selection of Spanish types for improved quality and adaptability to the Southwest.	F. Garcia.
New York (Cornell):		
Bean (chiefly field types).	Hybridization of varieties followed by pedigreed selection for development of disease-resistant varieties. Inheritance of resistance to specific diseases. Minor attention to inheritance of other characters. (Early work on inheritance of qualitative and quantitative characters.)	W. H. Burkholder, R. A. Emerson, A. L. Harrison, D. Reddick. (M. F. Barrus, W. H. Burkholder, G. P. McRostie, R. A. Emerson).
Cabbage	Improving variety uniformity and quality by selection. Developing new and superior combinations of characters by hybridization and selection. Inheritance of color, stem length, head shape, texture, and flavor (odor). Intertype crosses involving cabbage, cauliflower, brussels sprouts, kale, kohlrabi, and wild cabbage for cytogenetic study.	C. H. Myers, W. I. Fisher.
Celery	Inheritance of color; size, shape, and toughness of petioles; resistance to yellows.	R. A. Emerson.
Lettuce (cooperation with Department).	Selection within hybrid progenies and varieties for improved heading, quality, and tipburn resistance.	J. E. Knott, (J. B. Hartmann.)

Table 6—*Recent vegetable breeding activities of State and Federal agencies in the United States*—Continued

State or department and crop	Nature of studies	Personnel
New York (Geneva)		
Bean (snap)	Varietal crosses to obtain mosaic resistant improved sorts Inheritance of mosaic resistance	A L Harrison, J G Horsfall
Cucumber	Varietal crosses to obtain improved greenhouse types	W T Tapley
Cucurbita spp	Interspecific hybrids among *C maxima*, *C pepo*, and *C moschata* to determine specific limitations within the genus and possibilities of developing new and valuable combinations of characters, including disease resistance Inheritance of mosaic resistance	G P Van Eseltine
Muskmelon	Hybridization to obtain earlier and higher quality varieties	W D Enzie
Pea	Inheritance of root rot resistance	A L Harrison, J G Horsfall
Squash	Hybridization to obtain earlier and higher quality varieties	W D Enzie
Sweet corn	Development of new inbreds for production of superior hybrid corns for canning and market Chemical studies of hybrids	P V Traphagen
Tomato	Selection and varietal crosses for improved canning varieties adapted to the Northeast	C B Sayre
North Carolina		
Lettuce (cooperation with Department)	Selection within hybrid progenies and varieties for improved heading quality, and tipburn resistance	Robert Schmidt
Sweetpotato	Hill unit selection for improvement of varietal type and yield	Do
Tomato	Hybridization and selection for resistance to bacterial wilt	Do
North Dakota		
Bean	Varietal hybridization and selection to obtain earliness disease resistance and improved regional adaptation Inheritance of earliness	A F Yeager, D H Scott
Muskmelon	Hybridizing of American and foreign forms to obtain earliness size, quality adaptation to the region	Do
Physalis (ground cherry)	Varietal crosses and selection to increase earliness yield and improve yellow color	Do
Squash (*Cucurbita pepo*)	Inheritance of hard rind flesh color rind color Isolation of better adapted strains through inbreeding and selection	Do
Tomato	Inheritance of uniform color determinate growth locule number, earliness fruit size Varietal crosses and selection to obtain high yield quality, and earliness in northern Great Plains area	Do
Watermelon	Inbreeding and selection of heterogeneous foreign introductions to obtain varieties adapted to the region	Do
Ohio		
Beet	Sib mating of inbred selections to obtain superior color and absence of zoning in cannery beets	I C Hoffman, H D Brown
Cabbage	Inbreeding and selection to obtain more uniform and productive strains of Golden Acre	Do
Lettuce	Selection for tipburn resistance in greenhouse strains of Grand Rapids	Do
Tomato	Selection of greenhouse strains of Marhio	Do
	Interspecific crossing and backcrossing to obtain cladosporium resistance	L J Alexander
Oklahoma		
Sweetpotato	Hill unit selection in Nancy Hall and Porto Rico for increased yield, uniformity, and typical shape	E F Burk
Pennsylvania		
Cabbage	Line selection for higher yield, uniformity, and better storage quality	C F Myers, H K Fleming
Tomato	Inheritance of skin and flesh color in the Orange tomato Varietal crossing and selection for improved earliness, fruit shape, uniformity, and yield	Do
Puerto Rico (University station)		
Cucumber	Inbreeding, crossing, and selection for downy mildew resistance and adaptation to tropical conditions	A Roque
Eggplant	Inbreeding, crossing, and selection for resistance to bacterial wilt, for superior quality, and adaptability	Do
Tomato	Hybridization of commercial and native varieties for resistance to bacterial wilt and for improved adaptability and shipping qualities	Do
Puerto Rico (Federal station)		
Sweet corn	Inbreeding, crossing, and backcrossing sweet and native field types for resistance to stripe and to earworms, for good quality and adaptation to the Tropics	R L. Davis.

Table 6.—*Recent vegetable breeding activities of State and Federal agencies in the United States*—Continued

State or department and crop	Nature of studies	Personnel
Rhode Island:		
Eggplant	Pure-line selection, hybridizing varietal inbreds, and selection to develop wilt resistance in good commercial types.	T. E. Odland, F. K. Crandall.
South Carolina:		
Asparagus	Selection to obtain higher yield, uniformity, and adaptation to South Carolina conditions.	J. B. Edmond, L. E. Scott.
Bean	Intervarietal crosses and selection to obtain increased yield, tolerance to mildew and mosaic, earliness, tolerance to adverse growing conditions in South Atlantic areas.	J. M. Jenkins, Jr.
Okra	Pure-line selection for improved uniformity, quality, yield, and spineless pods.	R. A. McGinty, F. S. Andrews.
Sweetpotato	Hill unit selection for improved yield and uniformity	J. B. Edmond.
Tennessee:		
Tomato	Selection for fusarium wilt resistance	(S. H. Essary), C. D. Sherbakoff, B. D. Drain.
Texas:		
Onion	Selection for resistance to pink root and freedom from splits.	L. R. Hawthorn.
Peanut	Pure-line selection for increased yield, earliness, and oil content of Spanish type.	G. T. McNess.
Tomato	Intertype and intervarietal crosses and selection to develop freedom from puffy fruits. Inheritance of tendency to puffiness.	J. F. Wood, L. R. Hawthorn, S. H. Yarnell.
Sweet corn	Production of sweet corn adapted to Texas	P. C. Mangelsdorf.
Utah:		
Celery	Selection for uniform type and resistance to wilt in Utah variety.	A. L. Wilson.
Onion	Inbreeding and mass selection to improve yield, uniformity of shape, and keeping quality in Sweet Spanish.	Do.
Tomato	Selection to improve uniformity and obtain wilt resistance in Greater Baltimore and Stone types adapted to Utah conditions.	Do.
Vermont:		
Squash	Inbreeding Hubbard squash to improve uniformity, quality, and yield.	M. B. Cummings, E. W. Jenkins.
Virginia:		
Bean	Hybridization and selection for rust resistance, high yield and quality. Inheritance of rust resistance.	S. A. Wingard.
Peanut (cooperating with Department).	Pure-line selection to obtain high yielding very large-seeded strains of Virginia type.	E. T. Batten, J. H. Beattie.[1]
Virginia (Truck station):		
Kale	Pure-line selection for deeper green color and resistance to cold.	H. H. Zimmerley.
Spinach	Varietal hybridization and selection for resistance to cold, heat, mosaic ("blight"), and quick bolting; high yield and attractive savoy-leaved type.	(L. B. Smith), H. H. Zimmerley.
Washington:		
Tomato	Hybridization and selection to obtain early, locally adapted sorts.	C. L. Vincent, L. K. Jones.
West Virginia:		
Watermelon	Inheritance of resistance to certain forms of *Fusarium niveum*. Crossing and backcrossing nonedible resistant and edible susceptible forms to obtain edible resistant variety. Cytological studies of above material.	(L. S. Bennett), T. C. McIlvane, J. A. Rigney.
Wisconsin:		
Bean	Hybridization and selection to obtain mosaic-resistant snap beans of high quality and adaptation to Wisconsin.	J. C. Walker, W. H. Pierce.
Broccoli (sprouting)	Mass selection for improved head size and uniformity	O. B. Combs.
Cabbage (cooperating with Department).	Inbreeding and selection for yellows-resistant strains of the several commercial types. Determination of genetic nature and inheritance of different types of resistance.	(L. R. Jones, L. M. Blank), J. C. Walker.
	Inbreeding and selection for club-root resistance in crucifers.	J. C. Walker, R. H. Larson.
Eggplant	Hybridization and selection for increased size and earliness.	O. B. Combs.
Onion (cooperating with Department).	Hybridization and selection for smut resistance in onions.	J. C. Walker, H. A. Jones.

[1] Of U. S. Department of Agriculture.

TABLE 6.—*Recent vegetable breeding activities of State and Federal agencies in the United States*—Continued

State or department and crop	Nature of studies	Personnel
Wisconsin—Contd.		
Pea	Hybridization and selection for obtaining more productive, higher quality wilt resistant peas adapted to Wisconsin conditions	F J Delwiche (E J Renard)
	Inheritance of rogues	(F J Renard)
	Inheritance of resistance to fusarium wilt	(B L Wade)
Radish	Mass selection to improve uniformity and earliness of Scarlet Globe	O B Combs
Tomato	Hybridization and selection to improve fruit size and fruit setting under greenhouse conditions in winter	Do
Department of Agriculture		
Bean (snap and field)	Hybridization and selection among wide range of types to obtain	
	(1) Curly top resistance in garden and additional field types	(W W Tracy Jr)[1] B F Dana
	(2) Resistance to mosaic, rust bacterial blight and root rot in market, canning and field types	B L Wade W J Zaumeyer C F Poole, L L Harter
	(3) 'Multiple' resistance to all known strains of anthracnose	C F Andrus
	Inheritance of mosaic resistance (cooperative with Wisconsin)	(M C Parker)
	Inheritance of resistance to rust, blight and mosaic	B L Wade C F Poole, W J Zaumeyer
Bean (lima)	Inheritance of plant habit and seed coat color and pattern Varietal hybridization and selection to obtain increased setting of pods in the large seeded types increasing thickness and number of seeds per pod in small seeded types increased earliness	Roy Magruder
Beet	Development of highly self fertile inbred strains of good commercial type to improve uniformity and facility of maintaining varietal or strain characteristics	Do
	Inheritance of a variegated red color in the root	Do
	Crossing garden and curly top resistant sugar beet and selection to obtain curly top resistant garden varieties	B F Dana
Cabbage	Inbreeding and hybridization and selection to obtain a round, short core high quality, winter hardy non bolting variety for the South Atlantic and Southeastern States (See also Wisconsin, cabbage)	B L Wade C F Poole
Cucumber	Inbreeding and hybridization and selection among American and Asiatic types to obtain good commercial slicing and pickling varieties resistant to mosaic, bacterial wilt, and downy mildew 'Multiple' resistance is ultimate object	W S Porte S P Doolittle
Lettuce	Hybridization among American and foreign sorts and selection to obtain	
	(1) Resistance to brown blight and powdery mildew and adaptability to numerous different specific southwestern and Pacific coast conditions	I C Jagger T W Whitaker
	(2) Hard heading properties, high quality, resistance to tipburn and adaptability to eastern United States conditions (See also Massachusetts New York, and North Carolina, lettuce)	R C Thompson
	Inheritance of different anthocyanin and green leaf colors, seed color, chlorophyll deficiency, and tipburn resistance	Do
	Inheritance of resistance to brown blight and mildew	T W Whitaker I C Jagger
Muskmelon (in cooperation with California)	Hybridization and selection among American and Asiatic types to obtain varieties resistant to powdery mildew and of high culinary and shipping quality for the Southwest	I C Jagger T W Whitaker (J T Rosa[1] and G W Scott, California)
	Inheritance of resistance to powdery mildew	Do
Pea (part of program in cooperation with California, 1933–36)	Hybridization and selection among available peas of the world that indicate the desired characters, to obtain	B L Wade, W J Zaumeyer (H A Jones California)
	(1) Large podded market types resistant to fusarium wilt, to *Ascochyta*, and to adverse climate	Do
	(2) Resistance to certain mosaics	Do
	(3) Resistance to root rot	Do
	Inheritance of resistance to root rot certain mosaics *Ascochyta*, and certain new fusarium wilts	Do

[1] Deceased

TABLE 6.—*Recent vegetable breeding activities of State and Federal agencies in the United States*—Continued

State or department and crop	Nature of studies	Personnel
Department of Agriculture—Continued.		
Sweet corn	Development of varieties and of inbreds for production of hybrid corns. Objectives: High yield, uniformity, quality, adaptation to the Corn Belt, resistance to bacterial wilt, and specific kernel characteristics adaptable to factory use. Inheritance of quality in sweet × dent crosses. Inheritance of resistance to bacterial wilt, and of albescence.	G. M. Smith (in cooperation with Indiana).
	Hybridization and selection to obtain earworm resistant varieties adapted to the Southeast.	C. F. Poole.
Sweetpotato	Hybridization and selection as well as growing seedlings from open-pollinated seed to obtain variants of higher yield, starch content, earliness, quality, disease resistance or adaptability to specific environments. (Cooperative with La Estacion Experimental Agronomique, Santiago de las Vegas, Cuba; and Federal Experiment Station, Mayaguez, Puerto Rico.)	J. H. Beattie, C. E. Steinbauer, W. K. Bailey (Puerto Rico), (C. de Valle, Cuba).
Tomato (part of program in cooperation with Florida).	Inbreeding and varietal and interspecific hybridization and selection for resistance to wilt, nailhead, and various leaf and virus diseases, and to cracking; for high color, adaptability to shipping, and to specific adverse environments. Inheritance of resistance to wilt.	W. S. Porte, F. L. Wellman, B. L. Wade, C. F. Poole, (W. M. Fifield, Florida).
Watermelon (part in cooperation with California).	Study of seed size and color, flesh and skin color, size of fruit, and growth habit. Resistance to wilt, leaf diseases, weather conditions, and insect damage.	C. F. Poole, (D. R. Porter, California).

TABLE 7.—*Vegetable breeding and improvement work in foreign countries*

NOTE.—The limitations of this very sketchy survey are recognized. Only a part of the world's vegetable breeding activities have been referred to, and important activities have been unavoidably omitted. These few notes, however, testify to the world-wide importance of many general problems and the determination of plant breeders and vegetable growers to obtain ever better crop plants.

Country, institution, and official	Crop	Nature of studies
Australia, Department of Agriculture of New South Wales, Sydney; H. Wenholz, director of plant breeding.	Bean, broad	Adaptation studies of foreign introductions.
	Bean, snap	Hybridization and selection for higher yield, better adaptation and resistance to bacterial blight, anthracnose, mosaic, and dry root rot. Canadian Wonder × Refugee H. 3263 (U. S. D. A.) and Canadian Wonder × Murunga are promising unfixed early disease-resistant hybrids. Tweed Wonder × Keeney Refugee is a promising fixed early blight-resistant hybrid. New variety introduced: Hawkesbury Wonder, from Tweed Wonder × Keeney Refugee. Best yielding varieties are Canadian Wonder (standard), Hawkesbury Wonder, Staley's Brown Beauty, and Staley Surprise. Location: Hawkesbury Agricultural College; Bathurst and Grafton Experiment Farms.
	Beet, garden	Selection in self-fertile and close-fertilized lines for improved quality and yield. Best lines to date are from Rapid Red, Ohio Canner, and Detroit Dark Red (from United States). Location: Hawkesbury Agricultural College.
	Beet, silver, or chard	Selection, isolation, and testing of strains; self-fertility being sought; to improve uniformity and type of commercial varieties. Superior strains isolated from local silver beet and Lucullus. Begun 1930. Location: Yanco Experiment Farm.
	Cabbage, cauliflower, brussels sprouts.	Introduction of foreign varieties, testing, strain selection and purification of adapted commercial types. No controlled pollination used, but natural hybrids utilized when of value. Location: Bathurst Experiment Farm.

Table 7.—*Vegetable breeding and improvement work in foreign countries*—Continued

Country, institution, and official	Crop	Nature of studies
Australia, Department of Agriculture of New South Wales, Sydney; H. Wenholz, director of plant breeding.	Celery	Introduction of foreign varieties, testing against local varieties. Utah, Fordhook, and Pascal (commercial United States) and inbreds of Golden Phenomenal, Golden Self Blanching, and Golden Plume (California Agricultural Experiment Station) were most promising.
	Cucumber	Varietal crossing and selection for improvement of uniformity and adaptability of commercial slicing and of "apple" types; inbreeding for mildew resistance; attempts to cross *Cucumis sativus* (susceptible) with *C. anguria* and *C. metuliferus* (resistant) failed. New variety produced: Richmond Green Apple by crossing commercial × Apple. Location: Hawkesbury Agricultural College.
	Lettuce	Introduction and adaptation studies of foreign varieties, followed by selection and breeding. Best introductions for winter crop, Imperial F and Imperial 615 (U. S. D. A.); for summer, Iceberg (United States), and Imperial F. Local variety Yarrimundi is a pure green selected from an Iceberg stock; some resistance to "slimy heart." Location: Hawkesbury Agricultural College.
	Muskmelon	Introduction and adaptation studies of foreign varieties (United States best source of material; Spanish Gold, a Honey Dew type from France, is promising). Varietal crossing and selection for resistance to powdery mildew, using the California-U. S. D. A. mildew-resistant strains with susceptible sorts of high quality; also seeking downy mildew resistance. Location: Yanco Experiment Farm.
	Onion	Objects: To obtain earlier, better storing, more attractive adapted strains free from bolting and thick necks; also resistance to thrips and disease. Dominant varieties grown: Hunter River Brown and Maitland White. Location: Bathurst Experiment Farm and Hawkesbury Agricultural College.
	Pea	Varietal hybridization and selection for good agronomic characters plus resistance to *Fusarium martii* and *Mycosphaerella pinodes*. Most promising hybrid is Yorkshire Hero × Greenfeast. Location: Hawkesbury Agricultural College; Bathurst and Yanco Experiment Farms.
	Peanut	Testing and selection from large number of introductions, varieties, and strains for large-seeded Valencia or Virginia type with light-pink seed coat. Important Javanese introductions of Spanish type are Toeban and Tannah. Location: Grafton Experiment Farm.
	Rhubarb	Study of introductions and selection of seedlings of introductions and local varieties. South Australian Solid Red, a local variety of excellent color, is most valuable producer of promising seedlings. Location: Hawkesbury Agricultural College and Grafton Experiment Farm.
	Squash and pumpkin	Introduction, selection, and hybridization to obtain well-adapted high-quality varieties of uniform size and shape. Varieties released: Ideal, Satisfaction, and two introductions from the United States, Kitchenette Hubbard (Minnesota Agricultural Experiment Station) and Table Queen. Location: Grafton Experiment Farm.
	Sweet corn	Hybridization and selection to obtain high-yielding, vigorous-growing, high-quality sweet corn adapted to local conditions. New variety produced: Hawkesbury Sugar, from crossing dent and sweet types. Location: Hawkesbury Agricultural College.
	Sweetpotato	Production of seedlings from which desirable selections may be made. Seeds obtained from more tropical countries. Extensive introduction of foreign varieties.

TABLE 7.—*Vegetable breeding and improvement work in foreign countries*—Continued

Country, institution, and official	Crop	Nature of studies
Australia, Department of Agriculture of New South Wales, Sydney; H. Wenholz, director of plant breeding.	Sweetpotato	Best varieties: (Local) White Maltese, Wannop and Ashburn (introduced from the Union of Soviet Socialist Republics) N. 85. Location: Hawkesbury Agricultural College and Grafton Experiment Farm.
	Tomato	Introduction of foreign varieties and testing, varietal and species crosses and selection for following objects: (1) Early varieties for staking. Best introductions: Australian Earliana (a farmer's selection), Break o' Day (U. S. D. A.), and Potentate (from England). (2) Resistance to fusarium wilt, spotted wilt, and leaf mold or *Cladosporium fulvum*. Numerous crosses of Red Currant with commercial varieties. Some promising hybrids obtained, showing resistance to fusarium wilt: Australian Earliana × Break o' Day and Earliana × Red Currant. Latter resistant to spotted wilt. Leafmold-resistant strains by L. J. Alexander of Ohio being used in crosses. (3) Main-crop pulping varieties. Most promising hybrid: Red Pepper × Earliana. Varieties in current use: Norana (from north coast); Newport 4 and Master Marglobe (from United States). (4) Forcing varieties. Best current varieties: Planter's Favorite (a farmer's selection) and Potentate (from England). Location: Hawkesbury Agricultural College; Bathurst, Grafton, and Yanco Experiment Farms.
	Watermelon	Selection for good market type and resistance to fusarium wilt and anthracnose. New variety produced: Wilt Resistant Thurmond Grey, by selection from variety locally called Dark Seeded Grey Monarch. Location: Hawkesbury Agricultural College.
Brazil, Institute Agronomico do Estado de São Paulo, Campinas; C. A. Krug, head of genetics department.	Beans	Pure-line selection to improve stocks of main commercial varieties grown in Brazil. Varietal and species crosses to be made in breeding for regional adaptability and resistance to mosaic, anthracnose, and mildew (new work).
	Tomato	Introduced foreign varieties and local sorts studied for disease resistance and other valuable characters. Hybridization and selection will follow (new work).
Costa Rica, Department of Agriculture, Puntarenas; Alan Kelso, chief of propagation service.		Selection of several wild native or naturalized vegetable plants for adapting them to economic use; tomato and a number of leaf vegetables are included.
Czechoslovakia, State Institute for Horticultural Research, Průhonice; Ing. Fr. Landovsky, chief of division for vegetable and seed production.	Cabbage	Hybridization and selection for increased earliness, yield, quality, and improved local or special adaptations. Hybridization and selection for hardiness to permit overwintering in the open field. Promising selection from hybrid F_3 of Groots × Kärnten.
	Cucumber, onion	Selection for stock improvement in local varieties.
	Tomato	New variety produced: Průhonice, by crossing Lucullus × Tuckswood. Early, resistant to cracking, productive, high quality; for field or forcing.
	Radish	New variety produced: Průhonice, by crossing Triumph × Red Globe. Early (18 to 21 days) high quality, attractive; for field or frame forcing.
Plant Breeding Institute of Fürst Lichtenstein, Lednice; Fr. Frimmel, director.		Studies of hybrid vigor or heterosis are in progress, and hybrid seed or "heterosis seed" of tomato and spinach are produced on a large scale.
	Cucumber	Special interest in cucumber breeding. New variety produced: Zmojemska Nakladacka, a variety for the conserving industry.
	Tomato	Hybridization and selection with special reference to requirements of local growers and canners. New varieties produced: (1) Blondkopfchen, by crossing Yellow Cherry × Prinz Borghese. Grown for canning. More productive than Yellow Cherry. (2) Two other varieties, not named, by crossing Lucullus × Prinz Borghese and Coopers × Ficarazzi, respectively. For canning and market.

TABLE 7.—*Vegetable breeding and improvement work in foreign countries*—Continued

Country, institution, and official	Crop	Nature of studies
Plant Breeding Institute of Fürst Lichtenstein, Lednice, Fr Frimmel, director	Other vegetables	Beans for canning, red peppers, and melons ar receiving attention A number of commercial firms take special pride in their stocks of cucumbers, onions, kohlrabi, and celeriac or turnip-rooted celery
Denmark (Reported by Niels Esbjerg, State Experiment Station, Blangsted)		Research stations in Denmark are chiefly engaged in variety, strain and stock-testing, or seed-control work Vegetable improvement work is being done by commercial agencies, the resulting strains being submitted to Government agencies for recognition before going into trade channels State Experiment Station at Blangsted produced improved celeriac and is selecting cauliflower for cold resistance Selection and progeny testing is principal method used, with minor attention to hybridization Increasing work in disease-resistant selections largely on account of export trade to United States Some Danish firms reporting improvement work A Hansens, Kastrup—Cabbage, cauliflower, spinach, radish, and carrot Chr Olsen, Odense—Cabbage, cauliflower, kale, brussels sprouts, radish, carrot, lettuce, celeriac, spinach J C Helm Petersen & Co , Aarhus—Cabbage, carrot, beet, spinach, turnip-rooted parsley J E Ohlsens Enke, Copenhagen—Cabbage, brussels sprouts, kale, celery, radish, greenhouse lettuce, spinach, tomato, peas, snap beans Hybridization work with tomato, search for "velvet spot" resistance Hybridization with peas and beans Hjalmar Hartmann & Co , Copenhagen—Cabbage and cauliflower Union of Danish Cooperative Societies, Taastrup—Pure line selection of beans and peas Hybridization and progeny testing of cabb ge, beet, and pickling cucumber Progeny testing of onion, turnip-rooted parsley, radish, lettuce, spinach, and tomato
England		
Horticultural Research Station of Cambridge University, Cambridge, D Boyes, director	Broccoli	Production of Roscoff types of good curd texture, disease resistance, and adaptability to specific localities in England having different weather conditions
	Brussels sprouts	Object of work, to obtain varieties with small sprouts for canning or special markets, and varieties adapted to special conditions such as fen soils
	Cauliflower	Early, winter-hardy varieties are sought
	Onion	Production of English types for spring sowing and Spanish types adapted to England
	Parsnip	Production of half-long, smooth, white varieties for commercial use
	Pea	Production of new sorts for canning, hardy types for fall planting, and multipodded types Improved varieties produced have been privately distributed to supporters of the work (subscribers) and are not on the market
The Experimental and Research Station, Cheshunt, W F Bewley, director.		This station deals only with greenhouse crops
	Cucumber	Breeding for a short-necked disease-resistant variety
	Lettuce	Breeding for short-day types for winter culture
	Tomato	Breeding for high yield, quality, and resistance to *Cladosporium fulvum* Productions are distributed first to subscribers who support the research, later to general public Tomato E S 1 and Cheshunt Early Giant lettuce are in general cultivation
The Sealy-Hayne Agricultural College, Newton Abbot, Devon, F. R Horne, professor of botany	Winter cauliflower or broccoli	Intervarietal and intertype hybridization to obtain succession of maturity, sorts both earlier and later than those available Roscoff, Cornish, Angers, and Italian strains being used in breeding, although only first 2 are at present adapted to the environment Some promising hybrid progenies

TABLE 7.—*Vegetable breeding and improvement work in foreign countries*—Continued

Country, institution, and official	Crop	Nature of studies
Scotland, The Scottish Society for Research in Plant Breeding, Carstophine, Edinburgh, William Robb, director		Breeding and improvement work in progress upon swedes or rutabagas
Germany		
Versuchs- und Forschungsanstalt für Wein Obst- und Gartenbau Geisenheim, Professor Dr Rudolff, director	Tomato	Breeding and improvement work in progress
Institut für Pflanzenbau und Pflanzensuchtung der Universität, Halle Professor Dr Roemer, director	*Brassica* spp	Intertype and interspecific crosses studied with reference to fertility relationships and inheritance of specific characters with a view to possible value in future breeding work
	Beans, snap	Breeding for resistance to *Colletotrichum* in beans for canning
	Peas	Breeding work in progress for increased yield and earliness of sweet varieties
Kaiser Wilhelm Institut für Zuchtungsforschung, Muncheberg Professor Dr Rudorf, director	Rhubarb	Breeding work in progress for improved red color of petrioles, lower acid content, more upright growth, earliness, and disease resistance
	Tomato	Work in charge of Dr Sengbusch Intervarietal and interspecies crosses and selection (*Lycopersicon esculentum* and *L pimpinellifolium*) to obtain improved earliness, freedom from fruit cracking and leaf rolling, superior eating and keeping qualities, resistance to cold and *Cladosporium* Promising hybrids have been obtained and are being studied further
Gartnerlehranstatt der Landesbauerushaft Kurmark, Oranienburg-Luisenbof, Dr Bonhert, agricultural adviser	Kohlrabi	Breeding for late frost resistance high quality, small leaves, earliness, is being started
	Tomato	Promising results are being obtained in breeding for increased earliness, resistance to fruit cracking, and *Phytophthora*
Staatliche Versuchs und Forschungsanstalt fur Gartenbau, Pillnitz Professor Schindler, director	Asparagus	Crossing of selected parent plants followed by selection for earlier, stronger growing, rust resistant, tender varieties of good flavor
	Caraway	Selection for improved seed setting, uniformity, earliness, bright seed color, high oil content
	Dill	Selection for higher quality, improved seed setting, uniformity of ripening
	Mustard	Selection for large seed, high oil content, earliness, and uniformity of ripening
Staatliche Lehr und Forschungsanstalt für Gartenbau, Weihenstephan, Professor Bickel, director	Brussels sprouts	Improvement in winter hardiness, earliness, and uniformity of growth and bud formation
	Cabbage	Improvement in growth and head formation, storage qualities, solidity, and head leaf color
	Kohlrabi	Breeding white forcing varieties with more tender flesh, improved form, upright uniform leaves, earliness, resistance to cold
	Lettuce	Breeding for two different types (1) Very quick growing sort for forcing in hotbeds and (2) a larger slower growing sort for coldframes and open ground
	Tomato (forcing)	Breeding for rounder, brighter colored fruit, higher yield, and resistance to *Cladosporium* Resistance of practical value has been obtained, but improvement of fruit characters of such sorts must be continued
Japan, Imperial Horticultural Experiment Station, Okitsu, T Tanikawa, acting director	Asparagus	Testing and selection of promising varieties and strains Data for 1927 to 1936
	Brassica sp	Fundamental research in genetics with special reference to sterilities, compatibilities, effects of inbreeding, and studies of hybrid vigor (1924–32)
	Eggplant	Hybridization and selection for resistance to "blue rot", improved yield, uniformity, and quality Several promising strains obtained (1925 to date)
	Pea	New work started in breeding canning varieties adapted to Japan, by hybridization and selection Also fundamental research in genetics (1935)
	Tomato	New work started for production of new varieties for Japan, for market purposes

Table 7.—*Vegetable breeding and improvement work in foreign countries*—Continued

Country, institution, and official	Crop	Nature of studies
Mexico, Instituto Biotecnico. Work at numerous locations. Reported by G. Gandara.	Bean	Obtained a thick-rooted hybrid variety, Campotillo, from Spanish variety of *Phaseolus vulgaris* crossed with Mexican variety of *P. coccineus*.
	Cucurbita sp.	Acclimatization studies of different varieties.
	Tomato	Studies of factors responsible for association of red and yellow color with certain quality characteristics as sweetness or acidity.
	Other vegetables	Acclimatization and disease resistance studies being made on numerous local and introduced varieties of broadbean, chickpea, peanut, muskmelon, and watermelon.
Norway, Government Experiment Station in Vegetable Culture, Kvrthamar, St. Jordal; A. H. Bremer, director. (This station succeeded the former institution known as The Garden Cultivation Friends Experiment Station in 1919.)	Bean, pole	Pure-line selection for early, productive green and wax pole types that can be profitably grown in Norway. Erstling only successful variety at present, yields 30 percent more than any dwarf type tested. Expect to release 1 or more new varieties in 1937.
	Cucumber	Hybridization and selection for very early varieties of acceptable form and quality adapted to Norway. Commonly grown early variety, Muromsk, has low quality and good yield. Is being crossed with high-quality Russiskdrue and Reinische Vargebirge.
	Lettuce	Hybridization of varieties of differing responses to day length to obtain varieties adapted to short, long, and rapidly changing day lengths.
	Muskmelon	Cannot be grown in the open. Hybridization and selection for varieties adapted to forcing under Norwegian conditions.
	Pea	Pure-line selection started by K. Weydahl in 1915 led to introduction of stocks of 6 well-adapted strains in 1922, namely, Engelsk Sabel, Witham Wonder, Ne Plus Ultra Marrow, Saxa, Burton Snabel, and Early June. Hybridization and selection for better adapted types, accompanied by genetic studies; linkage shown between tall plant and parchment in pod with 4 to 5 percent crossing over. Two dwarf large-pod, parchment-free sorts introduced in 1929—Karl Weydahl and Bremers Marrow Sugar. Bremers Early Sugar selected from Sabel × Saxa released in 1931. Numerous hybrids at hand and genetic studies in progress.
(Historical notes on Norwegian vegetable varieties based on information furnished by Prof. Olav. Moen, of the Agricultural High School, Aas.)		Norwegian varietal improvement offers particular difficulties because of the far northern location and the sharp climatic contrasts existing within short distances, as coast and valley versus mountains; and windward versus leeward sides of the mountains.
	Bean	Skard selected an earlier bean than Erstling from Reistad. Grau obtained Olsak by varietal hybridization, also wax beans named Oslo Taro and Smarbukk. Bergsgubber is a Norwegian selection from Nordstjernen.
	Cabbage	Norwegian stocks of Amager are distinct and the results of numerous growers' selections for adaptation to specific conditions. Various strains as Berby, Amot, Fales Blatopp, Sandveds, Toten, and others. Moens Kvitkal result of many years' selection. Rossebo, Jatun, Stavanger Torv, and Jatunsalgets Vinterkal are results of varietal crossing.
	Pea	Chr. Olsen started wrinkled-pea improvement by selection in 1830, and many of present best varieties believed result of his work, as Grimstead Gartneris, Handes, and Bakkes.
	Tomato	Lund has developed an outdoor strain of Danish Export and of Hannestad, and a forcing strain of Kondine for Norway conditions.

TABLE 7.—*Vegetable breeding and improvement work in foreign countries*—Continued

Country, institution, and official	Crop	Nature of studies
Sweden:		
Agricultural Experiment Station, Alnarp; Carl G. Dahl.	Bean	Hybridization and selection for improved yield earliness, quality, and adaptabity to Sweden; strains 3 to 5 days earlier than any known sort obtained. also high-yielding wax sorts. All require further selection before introduction.
	Brussels sprouts	Hybridization and selection for high yield and cold resistance; work in progress.
	Cabbage	Common × savoy cabbage crosses made for milder flavor, good storage quality, and high yield. Alnarp cabbage No. 1 and Alnarp cabbage No. 2 released to the trade.
	Pea	Hybridization and selection for high-quality, high-yielding, large-podded, sweet, wilt-resistant peas for home, market, and canning. Many promising lines obtained. Alnarp Sten's No. 1 and Alnarp Sten's No. 2, released to the trade in 1927. They are high yielding and wilt resistant. Alnarp Sabel is a selection from Sabel. Numerous strains will soon be ready for release.
Horticultural Institute of W. Weibull & Co., Weibullsholms, Landskrona; H. Lamprecht, head of technical staff.		Selection and hybridization to obtain high-quality, early, productive varieties adapted to Swedish conditions of culture and use.
	Bean, snap	Stella, selected from strain grown on an old farm in Sweden, introduced to the trade about 1925. Early, thin hull, high yield. Alabaster II obtained through pedigree selection from Swedish variety Upplands; resistant to pod spot. Express, a wax variety introduced in 1932, was obtained by crossing German variety Daddel with an unknown. Very early and high yielding.
	Carrot	Regulas, a superior storage carrot, of qualities otherwise similar to Chantenay.
	Cauliflower	Giant Swedish No. 147. Obtained from cross of Giant Danish and an unnamed variety. Somewhat drought-resistant.
	Cucumber	Perseus, developed from Rockford. Earlier and more productive.
	Pea	Nanna, a sugar type, obtained from cross of Furst Bismarck × a red-flowering sort similar to Gray Giant. High yield, quality, and good adaptability. Extra Rapid, selected from Rapid, which is uneven in earliness. Said to be earliest pea grown. Released in 1927. Sylva, a marrow pea, was selected from Fairbeards Nonpareil, beginning in 1918. Released in 1925. Luna, an edible podded sort, from cross of Roi des Gourmands and Witham Wonder.
	Spinach	Valkyria II was selected from Valkyria and introduced in 1925. The plants are monoecious, high-yielding, resistant to *Peronospora*. Color somewhat light. Herta is dark green, dominantly but not completely monoecious, quick growing. Derived from cross of Valkyria and Victoria.
L. Daehnfeldts and G. Hylten-Cavallius, seedsmen, Halsingborg; Ernst Nilsson, in charge.		Varietal crossing and selection to develop high-yielding, high-quality strains and varieties adapted to conditions in Sweden. Varieties introduced to the trade as indicated.
	Bean, field	Risbrinken, selected from unnamed variety. Early and resistant to pod spot. Dwarf Brown, introduced in 1933, from cross between Nordstern and a brown variety in 1919. Said to be very hardy and adapted to northern Sweden.
	Bean, wax	A pedigree selection of Beurré Nain Sans Rivale adapted to Swedish conditions.
	Pea	Sugar types as follows: Norrlands, from Pilot × Bismarck; Early Giant, from Sabel × Laxton; Elitsabel, from Sabel × King; Giant Sabel, selected from English Sabel; Giant Sabel Elit, from Stens × English Sabel; Kings, a selected strain of Roi des Gourmands; Improved King, from Giant Sabel × King. Numerous strains of marrow and sugar peas are in process of development, principally by varietal crossing and selection.

TABLE 7.—*Vegetable breeding and improvement work in foreign countries*—Continued

Country, institution, and official	Crop	Nature of studies
Union of South Africa, Division of Plant Industry, Nelspruit, East Transvaal.	Bean Tomato	Breeding for resistance to blight and bacterial wilt. Breeding for resistance to wilt.
Union of Soviet Socialist Republics.		Unfortunately, up-to-date information from plant breeders in the Union of Soviet Socialist Republics could not be obtained in time for including in this report, but it should be pointed out that they are among the most active workers in the field today. Special emphasis has been placed on thorough exploration of all promising parts of the world for obtaining varieties and breeding material of value. Very extensive programs are in progress at numerous locations for studying introduced materials in detail and for large-scale hybridization and selection work. Large resources and great energy are being devoted to this work. There is no doubt that results of considerable practical and scientific importance are being obtained.

IMPROVEMENT OF SWEET CORN

C. F. POOLE, Cytologist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry

THE only genetic difference between the composition of a sweet corn kernel and that of field corn is due to a single recessive gene out of the hundreds or thousands of genes in corn. This gene makes the sugary condition of the kernel persist in sweet corn; or, in other words, prevents the conversion of some of the sugar into starch.

The first recorded observation of sweet corn by white men appeared in 1779, when Lt. Richard Bagnall, of Sullivan's Indian Expedition, returned from an Indian campaign to the west of the Susquehanna with several sugary kerneled ears procured from the natives. We know today that the Iroquois Indians cultivated at least two sweet varieties, one white and one black—similar to Black Mexican—and that the Indians of the upper Missouri included four sweet corns among the 104 corn varieties they cultivated (*45*).[1]

In 1828 Thorburn's seed catalog listed a single sweet corn variety, and by 1881 the number of advertised varieties in all seed catalogs had increased to 16. Today, by reason of an increased interest in the production of hybrid sweet corn, it would be difficult to estimate with any accuracy the number of sweet corn varieties and stocks on sale, but it must run into many hundreds.

Considering its popularity, it may be surprising to some that the region of sweet corn cultivation is confined practically to southern Canada and the northern half of the United States. There are three reasons for this restricted distribution. (1) The period during which sweet corn kernels remain sweet after picking is of very short duration, and at the higher temperatures farther south the sugars are rapidly converted to starch. (2) The corn earworm, *Heliothis obsoleta* Fabr., is less injurious or is absent only in latitudes with winter temperatures low enough to prevent winter pupation of the larvae. Earworm injury in the Southern States is so great that the main dependence for roasting ears is the naturally more resistant field corn, including such varieties as Trucker's Favorite, Mexican June, and Tuxpan. These varieties, together with practically all the field corns of the South, have become relatively resistant to the corn earworm through natural selection extending over a long period. This fact is being used to good advantage (*38*) in converting some of the leading southern dents into highly resistant sweet corns by appropriate crosses. The third reason is much like the second, but in this case the condition is bacterial wilt instead of an insect. This disease is especially severe in the South,

[1] Italic numbers in parentheses refer to Literature Cited, p. 392.

and sweet corn varieties are much more susceptible in general than the southern field corns.

Prior to 1900, when the rediscovery by three European botanists of Mendel's paper on hybridization in garden peas aroused greater plant breeding activity than had hitherto been known, the literature of sweet corn breeding was confined to descriptions of variety tests. An examination of the experiment station bulletins around 1889, especially in Illinois, Indiana, and Nebraska, shows the names of some 75 sweet corn varieties classified according to earliness or lateness of maturity, color of kernels, and suitability for cultivation in those States. Some attempts were then made to standardize names and show which were synonymous. Early station bulletins from North Carolina and Louisiana mentioned that field corns were productive under local conditions, but sweet corn could not be successfully cultivated because of the damage inflicted by the corn earworm.

With few exceptions the men then practicing plant breeding failed to conceive of the possibility of hybridizing different stocks of corn with a view to producing new types for special purposes. Mendel's paper, however, by clearly stating certain definite laws of inheritance operating when character contrasts are introduced in a cross, showed that breeding for special purposes could be done systematically and with comparative ease. After 1900 the character of experiment station publications changed from lists of varieties to reports of crosses made with definite objectives, such as production of extra early maturing stocks, and of better canning varieties with deeper and more tender kernels, increasing the uniformity of all characteristics in canning varieties, and increasing yield and resistance to disease or insect attack.

WE CAN *hardly overstress the importance to the canned-corn industry of the all-embracing uniformity of characters resulting from the production of crosses and top crosses of inbred lines of sweet corn. The uniformity in texture and consistency of grains and in shape and size of ears has practically revolutionized the machinery and methods of handling in the cannery; and furthermore, in the field the even placing of the ears on the stalks and the uniformity with which an entire field reaches maturity have brought economies never before possible. These advantages are also evident in more recent cannery practices, such as putting up corn in frozen packs, and an increase in the whole-grain method of removing kernels from the cobs. It is estimated that about 80 percent of the yellow sweet corn grown for canning in 1937 will be from hybrid seed, and half of this, or 40 percent of all yellow cannery sweet corn, will be Golden Cross Bantam.*

Among the first sweet corn breeders to work for specific ends without knowledge of Mendel's laws was a Maryland physician, Stabler (*44*). In 1879 he planted alternate rows of Burr Mammoth and Stowell Evergreen and removed the tassels from the latter, thereby obtaining hybrid seed from which he selected an improved canning variety called Roslyn Hybrid Sweet. The new variety had large ears, straight rows, deep kernels, small cobs, and a higher yield than either parent. Stabler later produced an earlier maturing evergreen variety, called Early Stabler, by selecting seed from the first ears to set. He recognized that even though the ears were open pollinated, so that the pollen parent was unknown, it had to be early maturing to pollinate an early silking plant, and consequently the ensuing selections would be earlier than the original stock.

The interest aroused in genetics and plant breeding after 1900 was promptly applied to sweet corn, first by Halsted, Kelsey, and their colleagues in New Jersey, and later by East in Connecticut, Pearl, Surface, and Sax in Maine, and Huelsen and Gillis in Illinois. These workers established inbred lines through artificial self-pollination to produce true breeding stocks and to eliminate defective characters. With improved inbred lines they expected to analyze the factors of inheritance and produce newly constructed varieties from specifications found in both parent stocks. At about the time of the Maine work, Collins and Kempton (*7*), of the United States Department of Agriculture, made the first deliberate attempt to breed a sweet corn resistant to the corn earworm by crossing resistant dent varieties with susceptible sweet corn varieties.

SWEET CORN BREEDING

Sweet corn is chiefly used as a canning vegetable almost throughout the world and as a green garden vegetable in regions favoring its cultivation. The activities of sweet corn breeders are predetermined by these uses somewhat along the following lines:

1. For the canning industry, the production of high-yielding uniform hybrid stocks with good quality, by crossing inbred lines among themselves or top crossing inbred lines as pollen parents on commercial varieties as seed parents. Both practices insure greater uniformity in time of maturity, as well as in other characters, and increased yield.

2. Extension of the geographic range of the crop farther southward through the development of improved earworm-resistant varieties of sweet types by hybridization of susceptible varieties of good quality with naturally resistant field corns; and the extension of the range northward by selecting extra early maturing stocks.

Shortly before the timely rediscovery of Mendel's paper, Halsted and his coworkers (*13, 14, 15, 16, 17, 18, 19, 20, 21*) of New Jersey in 1898 began breeding sweet corn with the object of combining in one variety the best features of Black Mexican and Egyptian (Washington Market), which had white kernels. They observed that crossed seed in this case could easily be identified on ears of Egyptian plants, since corn has the advantage of exhibiting xenia.[2] For example, black aleurone color is dominant to clear in this cross, and any kernels on a plant with white ears that chance to be pollinated by pollen grains

[2] See the article on Fundamentals of Heredity for Breeders, in this Yearbook.

from a black parent will develop into black instead of white kernels. Black Mexican and white Egyptian occupied adjoining rows and the breeders commenced their work merely by choosing black seeds from Egyptian ears. Faster progress was made by raising a winter generation in the greenhouse, and in their earlier work Halsted and Kelsey selected breeding stock from open pollinated ears. It was not until 1900 that they practiced artificial pollination and not until 1905 that their reports began to include Mendelian terms. Notwithstanding their primitive methods at the beginning, the new variety Voorhees Red Sweet was fairly well fixed when it was released to the public in 1903. The variety combined features from the two parents and in addition exhibited red kernels, a character not expressed in either parent.

Immediately upon adoption of controlled pollination and Mendelian conceptions, Halsted began an extensive hybridization program with sweet corns with the specific object of improving stocks for earliness, higher percentages of two- and three-eared stalks, and recombination of the best features of diverse parents. At first Black Mexican was used as pollen parent with Malakov, an extra-early variety recently introduced from Russia, and with Garwood, Country Gentleman, Striped Evergreen, Banana, and Golden Bantam. Many other varieties were included later, and Black Mexican was omitted when pollination from bagged tassels made xenia no longer important as a device in this work to identify a cross. The problem of adequately testing the new stocks was overcome by enlisting the aid of cooperating farmers. In 1906, seed of six new varieties was widely distributed for trial and the year following four more were added to the number, two of which were given names abbreviated from the two parents, Malamo (Malakov × Premo) and Malakosby (Malakov × Crosby).

At this time Halsted began crossing sweet corns with Iowa Silvermine (white) and Pride of Nishna (yellow), dent corns, further to increase the yield of seed and stover. From the former he derived Silver Sweet by crossing with Stowell Evergreen and Jersey Sweet by crossing with Country Gentleman.

The order of importance of the elements that contribute to quality in sweet corn depends on whether we are considering market varieties or canning varieties. The market gardener places sweetness first, followed by tenderness of the pericarp, or outer covering of the kernel, then consistency or texture of the kernel contents. But since the canner may add extra sugar to the brine, his specifications for the breeder (*9*) place tenderness of the pericarp first and sweetness last, with consistency of kernel as the requirement second in importance.

Sweet Corn for the Cannery

The chief factors in the selection of varieties for use in the canning industry are deep kernels, yellow or white, according to local preferences; uniformity in all characteristics of the plant and ear; satisfactory yields; high quality; and, in regions afflicted with insects or disease, resistance to or escapement from injury. Previous to 1924, the date when practical interest was first aroused in the production of hybrid stocks from crossing inbred sweet corn lines, canned sweet corn was

obtained almost entirely from the four major varieties described in table 1.

TABLE 1.—*Sweet corns used for canning*

Variety	Year introduced	Color	Maturity date	Height	Cut corn at 20 days
				Feet	*Percent*
Crosby	1860	White	Early	5-6	37.2
Stowell Evergreen	1860	do	Intermediate	7-8	45.9
Country Gentleman	1882	do	Late	7	46.1
Golden Bantam	1900	Yellow	Early	5-6	27.4

The data shown as percentage of cut corn at 20 days after the appearance of the silks, as given by Culpepper and Magoon (*8*), are included in order to indicate the efficiency of a variety in producing the deep kernels best suited for canning. This figure is computed by dividing the weight of cut kernels by the total weight before cutting.

A serious drawback of all commercial varieties for canning purposes, however, is the great variability in characters, and especially in the time when individual plants reach maturity. This means that at any given time a large percentage of underripe and overripe ears must be taken, along with those in prime condition. A breeding practice that would increase the uniformity in reaching maturity, shape of ears, or texture of grains, as well as giving increased yield or greater depth of kernels, would be desirable. The increase in uniformity alone would be a great boon to the canning industry because this results in a relatively much larger pack from a given yield in the field. It was shown by G. H. Shull in 1908 that increased yield and a high degree of uniformity in all characteristics would result from crosses between inbred lines. Many years before this, about 1880, W. J. Beal, of the Michigan Agricultural College, observed that hybrid vigor and somewhat greater uniformity resulted from the crossing of commercial varieties in the field. At that time he proposed planting alternate rows of two field varieties, detasseling one and using ears from the detasselled variety to obtain hybrid seed.

MORE RECENT BREEDERS

In the summer of 1907 Pearl and Surface (*39*) in Maine commenced investigations on sweet corn for the specific purpose of producing seed adapted to Maine rather than to Connecticut and Massachusetts—the chief sources of seed. For the production of improved canning varieties their immediate objectives were greater earliness, higher yield, and improved ear shape. They produced inbred lines by inbreeding for several generations and discarded the poorer lines while retaining the better ones. Their contribution to sweet corn breeding practice was the selection of breeding stock on the basis of the performance of the progeny and not upon the appearance of the ear and plant, which had been the practice until that time. In their own words, "the objects of selection must be to discover and separate the desirable genotypes from the poor ones." After 3 years of such work Maine farmers had better locally grown seed than could be purchased elsewhere.

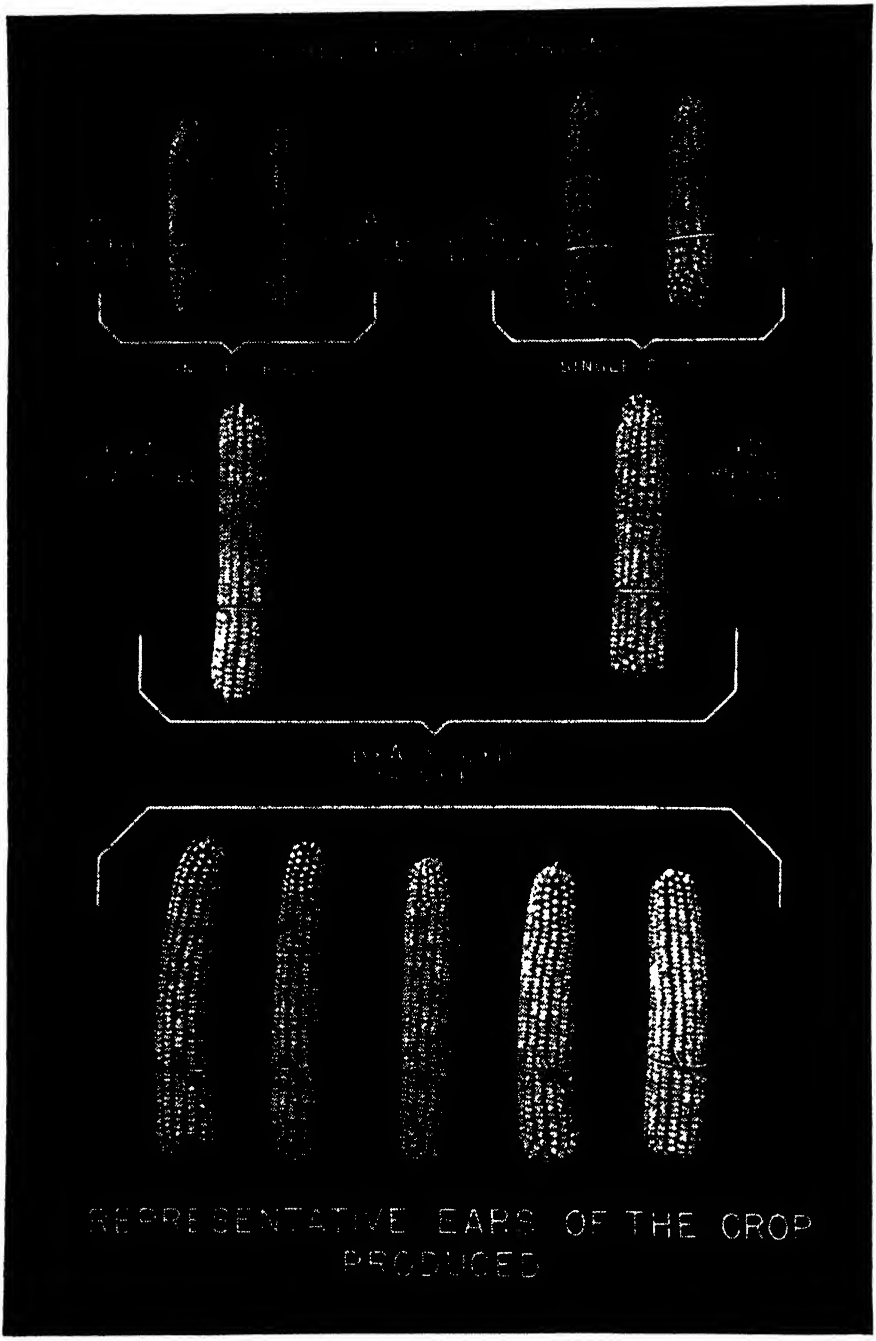

Figure 1.—**Method of producing double-cross hybrid seed corn and representative ears of the crop produced from hybrid seed.**

In Illinois, which, according to the latest statistics, is usually slightly ahead of Iowa as the leading sweet corn State, both in acreage and in total pack, breeding operations were begun about 1926 by Huelsen and Gillis, as reported by Keilholz (*32*). Their methods were much the same as those already in use elsewhere, but they emphasized the improvement of quality by use of the puncture test to identify the most tender lines for use in breeding. The test shows the pressure in grams per square centimeter required to penetrate the pericarp of the corn kernel. Huelsen and Gillis learned that high degrees of tenderness are exhibited in dent corns as well as in sweet corns.

In Connecticut the production on a commercial scale of cross-bred seed from inbred lines in field corn was first practiced in 1921 by George S. Carter, of Clinton (*30*). Shortly thereafter, in 1924, the Connecticut Agricultural Experiment Station introduced an F_1 or first-generation hybrid sweet corn called Redgreen, produced from two inbred lines, one being Stowell Evergreen and the other from a variety of unknown parentage. This hybrid stock was soon grown and canned by the W. N. Clark Canning Co., of Rochester, N. Y., and its superior characters in adaptation to locality, productivity, uniformity of maturing, and quality were immediately recognized.

Redgreen was not as successful elsewhere as in New England, central New York, and certain sections of the Northwest. Today practically every experiment station has several or many such cross-bred stocks, many of which are sold by the leading vegetable seedsmen. The lead in such activities was taken by the Connecticut station (*30, 31*), the Minnesota station (*28*), and the Purdue University station in cooperation with the United States Department of Agriculture. Figures 1 and 2 illustrate the methods and results obtained in producing single- and double-crossed corn.

The most popular and most widely adapted of these hybrid stocks is Golden Cross Bantam, produced about 1927 by Smith (*43*), of the Department, in cooperation with the Purdue University station by crossing Purdue 39 (Purdue Bantam) and Purdue 51, both inbred lines of Golden Bantam. Purdue 39 has attained some degree of commercial importance in its own right by reason of its resistance to bacterial wilt or Stewart's disease (*Aplanobacter stewarti* (E. F. Smith) McC.), high quality, and yield.

The great popularity of Golden Cross Bantam is chiefly due to its yield, canning qualities, uniformity, and resistance to bacterial wilt (figs. 3 and 4). This disease is most serious in latitudes close to 40° north and is of importance mainly in sweet corns, sometimes destroying almost the entire crop. The earlier maturing varieties are most susceptible. A recent study of Stewart's disease (*26*) recognizes two distinct genetic types of resistance: (a) Vigor-correlated, inferred from the fact that vigorous hybrids between some low-resistant inbred strains are more resistant than either parent; and (b) true resistance, shown by the fact that hybrids from low-resistant inbreds are less resistant than hybrids from high-resistant inbreds. Golden Cross Bantam may owe its high degree of resistance to both these causes, since it has hybrid vigor and one of its parents, Purdue 39, is also highly resistant.

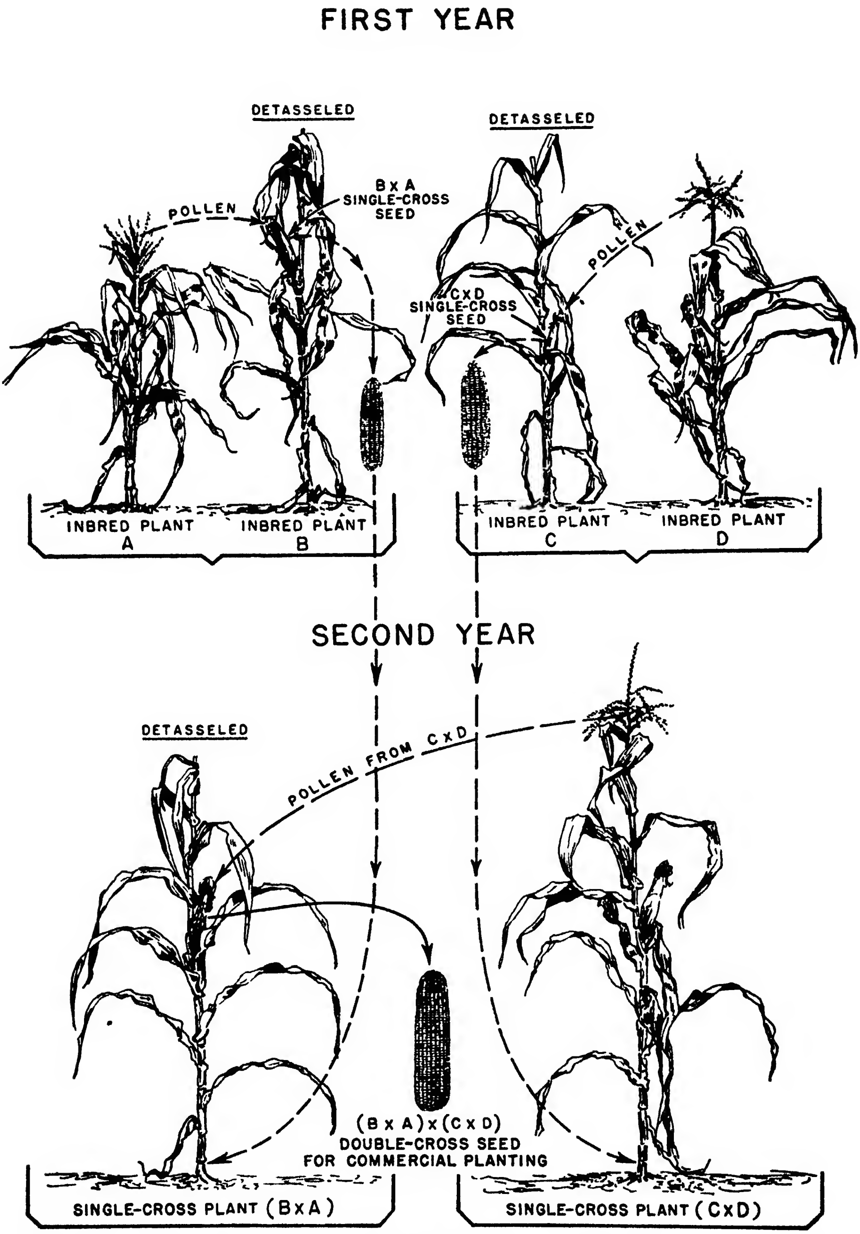

Figure 2.—Diagram of method of crossing inbred plants and the resulting single crosses to produce double-cross hybrid seed.

The tremendous importance of these hybrid sweet corns, and particularly Golden Cross Bantam, is indicated by the fact that it is estimated that about 80 percent of the yellow sweet corn which will

be grown for canning in 1937 will be grown from hybrid seed. It is estimated that half of this, or 40 percent of all yellow cannery sweet corn, will be Golden Cross Bantam

Figure 3.—Golden Cross Bantam, a variety resistant to bacterial wilt or Stewart's disease. It remains healthy on wilt-infected soil and makes a normal crop.

Top-Crossed Sweet Corn

The use of inbred lines as pollen parents crossed on commercial varieties as seed parents—called the top cross—for producing uniformly maturing and high yielding corn stocks was begun at the Connecticut Agricultural Experiment Station in 1917 with field corn The practice was soon used on sweet corn with excellent results, and

in 1935 the station recommended to the trade two early stocks, Spancross C–2 and Marcross C–6, and two midseason stocks, Whipcross C–6.2 and Whipcross C–7.2. In addition to these they recommended for the 1936 trade the following new top crosses: Marcross C–13.2, Burcross C–2, Sencross C–7, Dalecross C–2, Orcross C–2, Coincross C–2, and Stancross C–2. The 1935 seed catalog of one of the vegetable seedsmen listed four top crosses, all of which were produced by its own breeding staff. In recommending the top-cross method, Jones and Singleton (*31*) say:

Figure 4.—Golden Bantam, a variety susceptible to bacterial wilt, growing in infected soil near the plant shown in figure 3. Golden Bantam was practically a total loss in this test.

> From the standpoint of ease of producing seed and the adaptability of this seed, as compared to that of single crosses (between two inbred lines), there is much to be said in favor of variety-inbred crosses (top crosses)

The importance to the canned-corn industry of the all-embracing uniformity of character resulting from the production of crosses and top crosses of inbred lines can hardly be overstressed. The uniformity in texture and consistency of grains and in shape and size of ears has practically revolutionized the machinery and methods of handling in the cannery; and furthermore, in the field the even placing of the ears on the stalks and the uniformity with which an entire field reaches maturity have brought economies never before possible. These advantages are also evident in more recent cannery practices, like putting up corn in frozen packs and the whole-grain method of removing kernels from the cobs. In each instance the uniform texture of grain in single-cross and top-cross stocks of sweet corn makes them superior to the open-pollinated corn varieties.

Market Sweet Corn Breeding

Many of the varieties bred for the canning industry also are suited to market growing. In addition, there is need for extremely early strains for the extreme northern areas of the territory. In the South the question of earworm resistance is of major importance, and, if resistant strains are developed, sweet corn culture may increase in importance in this region.

About 1913 Collins and Kempton (*7*), of the Department, began a study on earworm resistance in dent and sweet corn. They obtained two highly resistant dent varieties, which were crossed with three susceptible sweet varieties, Stowell Evergreen, Early Evergreen, and Cory. The hybrid progenies proved more resistant than the commercial varieties. Prolongation of the husks beyond the tip of the ear and thickness of the husks were found to be associated to some extent with low damage. The evidence indicated that increased resistance of the hybrids also was due to other characters not measured but probably correlated with husk prolongation. The presence of some volatile substances distasteful alike to the moth and larva, but too elusive for measurement, was suggested.

Mangelsdorf, of Texas, crossed the highly earworm-resistant dent varieties, Mexican June and Surcropper, with the sweet variety Country Gentleman, and continued backcrossing to the dent parent for several generations. Eventually he obtained two varieties of sweet corn, Honey June and Surcropper Sugar, which to outward appearances were practically identical in plant characters with their dent parents and were highly resistant to the earworm, but which in addition were sweet. In numerous tests of the adaptation of these two sweet corns to conditions in Texas (*23*, *24*) and in California (*40*, *41*, *42*), the degree of earworm resistance has been demonstrated to be superior to that shown in any other sweet corn varieties with the possible exception of Papago, a commercially unpromising sweet corn produced by Freeman (*12*) at the Arizona station, and of Aunt Mary's Sweet.

Papago was produced from a few sweet grains found in the summer of 1910 on ears of squaw (flour) corn grown by the Papago Indians. Aunt Mary's Sweet is a recently introduced sweet corn from Ohio, which has been carefully nursed from year to year for perhaps a century on a single farm near Darby Plains. Such antiquity suggests Indian origin, and this is the expressed belief of the introducer, L. R. Bonnewitz, of Van Wert, Ohio. The point of Indian origin might well be stressed for Papago and Aunt Mary's Sweet, since it is to be expected that the inherent earworm resistance of maize varieties in possession of the Indians was due to a fixation by natural selection of resistance to earworm attack.

Florida 191 and Suwanee Sugar, recently produced by the Florida station, have given much promise as earworm resistant converted dent-sweet corns when tried in the diverse environments of the Southeast and the far West. More recently, Georgia 439 and Georgia 428 from the Georgia Experiment Station have indicated promise equal to that of the best strains of Honey June (*23*).

In the last 4 or 5 years a number of investigators in widely distant States have independently conducted tests of rather extensive lists of

varieties of sweet corn to determine their earworm resistance and value for market or breeding purposes. In tests at Davis, Calif. (*40*, *41*), Winter Haven, Tex. (*23*, *24*), and Charleston, S. C., certain varieties were consistently outstanding in earworm resistance, namely, Honey June, Surcropper Sugar, Papago, Aunt Mary's Sweet, Florida 191, and Oregon Evergreen. The relative resistance of these sorts varied among the several tests, but they were of the same general degree of resistance.

Even with the high degrees of resistance thus far uncovered, progress in breeding earworm resistant sweet corns is still far from satisfactory. Other hybrids have recently been made by Mangelsdorf in Texas (see the table of introductions in the appendix) and by Poole in California, using southern dent corns like Tuxpan and Davis Prolific that are even more resistant than the first dent parents used in producing Honey June and Surcropper.

Evidence obtained during 2 years of study by the California station has demonstrated, in statistically significant tests, that high earworm resistance is altogether independent of length or thickness of husks.

Other possible factors not correlated with resistance are length of ear, weight of ear, height of plant, and length of time required for maturity (*42*). Promising lines of investigation as yet untried include the search for factors determining volatile compounds that repel laying moths, suggested by Collins and Kempton, measurement of the tightness of the husk covering, and determination of the quality of husk covering. These lines of investigation will require collaboration with specialists outside the field of genetics, or the development of a special technique, before quantitative measurements can be taken.

Although it is still too early to estimate the extent to which these new sweet corns will extend the geographic range of sweet corn cultivation, there is no question regarding the interest of truck and home gardeners in present efforts. Honey June in particular has aroused enthusiasm among Texas and California growers, and one railroad company in Texas has planted large acreages for shipment of green sweet corn to northern points.

GENETICS [3]

THE genetics of sweet corn is the same as the genetics of corn in general, except for the particular genes responsible for the sugary condition of the endosperm. Corn genetics has been so adequately treated in the 1936 Yearbook of Agriculture (*27*) that no further reference is necessary except for considerations peculiar to sweet corn.

As has been said, the only genetic distinction to be drawn between starchy endosperm and sweet endosperm is the fact that the normal gene Su_1 (starchy) at locus 71 on chromosome IV (*10*) in field corn has mutated to su_1 (sugary) in sweet corn. There is another allelomorph of this gene at the same locus, and in addition two nonallelomorphic sugary genes on two other chromosomes than number IV, which will be discussed below. The sugary mutations result not only in a higher total sugar content but also in a persistence of the sugary condition of the endosperm to maturity. All other characteristics of the sweet

[3] This section is written primarily for students or others professionally interested in genetics or breeding.

corn varieties, such as short stature, early maturity, loose husks, etc., are shared in common with field corn.

The investigator who seeks to effect certain combinations between sugary or sweet corns and nonsugary corns may encounter aberrant monohybrid ratios involving the sugary character. These aberrant ratios are due in some cases to the action of genes linked with su_1, but also may be due to other causes (*2, 3, 4, 5, 6, 33, 34, 35*).

Mangelsdorf (*37*) investigated the respective rates of growth of pollen tubes carrying Su_1 and su_1 and finds that Su_1 pollen tubes have an accelerated growth rate at the start and that su_1 pollen tubes grow as fast as Su_1 when the initial handicap is overcome.

In most other cases reported in the literature it appears that when both *Su* and *su* appear together in one organism, the F_2 segregates in entirely normal monohybrid ratios. The first exception was noted in 1920 by Harper (*22*), who reported that when two sugary races were crossed the resultant F_1 was starchy, indicating two nonallelomorphic sugaries. Subsequent investigations have shown that there are indeed two previously unknown nonallelomorphic sugary genes, su_2 on chromosome VI (*11*) and su_3 on chromosome IX (Eyster, unpublished, *10*). Furthermore, there is some evidence that at the su_1 locus on chromosome IV there is a third member of the series, su_1^{am}, producing a sugary kernel not as sweet as su_1, and which apparently is associated with the presence of the gene *du*, dull endosperm, on chromosome X (unpublished communication from Mangelsdorf, also mentioned in *10*).

A condition called "pseudostarchy" has been analyzed by Jones (*29*) and is thought to be caused by the complex interaction of three dominant genes with the su_1 gene. One gene is necessary for the full expression of pseudostarchy, a second inhibits the shrinkage of sugary kernels, whereas the third dominant gene produces an opaque appearance of the dried kernels.

In an investigation of the chemical composition of known endosperm genotypes from crosses of dent × sugary, Lindstrom and Gerhardt (*36*) showed (table 2) an increase of sugars and a decrease of starches for each additional *su* gene (expressed as *s* in table 2) obtained in the recombinations resulting from reciprocal F_1 matings and backcrosses, or in an F_2 generation.

TABLE 2.—*Carbohydrate percentages for whole kernels (moisture-free basis) for different types of crosses and known genotypes*

Cross type [1]	Endosperm genotype	Samples	Total sugar	Dextrin	Starch	Carbohydrate index [2]
		Number	*Percent*	*Percent*	*Percent*	
White dent	*SSS*	3	2.3	1.9	56.6	0.07
Evergreen	*sss*	3	4.9	24.5	27.9	1.05
F_1 (HF × E)	*SSs*	4	2.7	2.1	53.6	.09
F_1 (E × HF)	*ssS*	1	3.6	1.7	56.1	.09
F_1 × E	*SSs*	4	1.8	1.6	57.5	.06
	sss	3	5.3	25.7	23.1	1.34
E × F_1	*ssS*	3	2.2	2.2	55.8	.08
	sss	2	4.5	25.9	27.1	1.12
F_2	*SSS*	4	2.3	2.7	57.5	.09
	sss	3	5.3	29.1	21.6	1.59

[1] HF = High fat strain; E = evergreen parent.

[2] Ratio of total sugar plus dextrin to starch.

In another analysis of chemical composition of known endosperm genotypes involving the sugary gene, Abegg (*1*) demonstrated a cumulative relationship for percentage of crude fat relative to the genes sugary and waxy in the following series:

Genotypes:	Percent of crude fat	Genotypes—Continued.	Percent of crude fat
Su su su Wx wx wx	1.0	*su su su Wx wx wx*	2.6
Su su su wx wx wx	1.4	*su su su wx wx wx*	3.0

The typical ear of corn possesses rows of kernels in even numbers because the female florets of the ear are arranged in pairs, each member of which has two ovules. The rows are straight because only one ovule on each floret develops, and the relatively uncrowded ear displays its kernels in an evenly rowed condition. The sweet corn variety Country Gentleman, however, is unique in the fact that the second ovule of each floret also develops and produces a crowded zigzag or "shoe-peg" condition. Huelsen and Gillis (*25*) investigated the inheritance of the apparently unrowed condition in Country Gentleman by carrying to the F_3 generation a cross between Country Gentleman and Narrow Grain Evergreen, the latter with typical straight rows. Intermediate degrees of zigzagging were sometimes difficult to classify, but on the whole the data conformed quite well to the working hypothesis that the unrowed condition of Country Gentleman was due to the operation of two pairs of recessive genes, $p_1\ p_1$ and $p_2\ p_2$, the chromosomal locations of which have not yet been identified. According to hypothesis the history of this cross is symbolically represented as Narrow Grain Evergreen, rowed $(P_1P_1P_2P_2)\times$ Country Gentleman, unrowed $(p_1p_1p_2p_2.)$

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POPCORN BREEDING

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POPCORN is a peculiarly American crop. Not only was it unknown to white men before the discovery of North America, as was all maize, but its cultivation and use for popping is almost entirely restricted to the New World. European visitors frequently express surprise at this unique form in which corn is available for human consumption.

It seems practically certain that popcorn was grown and popped by the Indians before the coming of Columbus. The records, although fragmentary, indicate that popped corn either whole or pulverized was used in native food dishes by various tribes in both North America and South America. Popcorn kernels and specially shaped earthenware dishes thought to be corn poppers have been discovered among prehistoric Indian remains in South America. In early Spanish writings, reference is made to the rituals of the Aztecs in which

> one hour before dawn there sallied forth all these maidens . . . crowned with garlands of maize, toasted and popped, the grains of which resembled orange blossoms, and on their necks thick festoons of the same which passed under the left arm.

BASIS OF POPPING BEHAVIOR

THE phenomenon of popping in corn is not limited to popcorn, but is exhibited to the greatest degree in this subspecies (*Zea mays* var. *everta* Bailey). Many flint corns under proper conditions will pop passably well, and some of the horny dents will occasionally pop a little. Even among the true popcorns there is a wide variation in the degree of popping. The ability to pop seems to be conditioned by the relative proportion of horny endosperm where the starch grains are embedded in a tough, elastic colloidal material, which confines and resists the steam pressure generated within the granule until it reaches explosive force.[1] Some varieties of sorghum with seed of a dense flinty structure, such as Pink kafir, pop very well. Manufacturers of breakfast cereals have perfected mechanical methods of confining steam pressure within grains until it is suddenly released, when they puff or pop to several times their original volume.

DISTRIBUTION, VARIETIES, AND DESIRABLE QUALITIES

COMPARED with dent corn, popcorn is a relatively minor crop. Only about 0.1 percent of the total corn acreage of the United States ordinarily is occupied by popcorn. It is grown almost solely for human consumption as freshly popped corn or as a basis of popcorn

[1] WEATHERWAX, P. THE POPPING OF CORN. Ind. Acad. Sci. Proc. 1921: 149–153. 1922.

confections. It has approximately the same chemical analysis and the same feeding value as dent corn. Thus, popcorn may be substituted for dent corn as feed for livestock if occasion demands, although the lower acre yield and the hardness of the endosperm, which necessitates grinding, make it uneconomical to do so under ordinary circumstances.

It is probable that popcorn is grown as a family garden crop for home consumption in every State in the Union. A very considerable proportion of the total popcorn production is represented by these small growers whose crop is used in the home or is sold only locally. A multitude of varieties, colors, and types of popcorn are used for this purpose.

Commercial production to supply vendors, manufacturers of popcorn confections, and the general retail grocery trade has been highly specialized and localized until the last 2 or 3 years. Sac and Ida Counties in western Iowa have been the principal center of commercial popcorn production. Valley County in central Nebraska and four or five counties in northeastern Kansas have also been important in commercial production.

Very recently Iowa, Nebraska, and Kansas seem to have been somewhat less important as centers of commercial production. This has been due in part to a changing demand, which in recent years has favored varieties too late to mature satisfactorily in northern regions, but more largely to the unprecedented series of disastrous droughts during the last few seasons that have centered around the traditional commercial popcorn region. As a consequence of crop failures, popcorn prices have been abnormally high, and therefore scattered growers in many localities outside the worst of the drought area have found popcorn growing very profitable during the years when the total production of the country was at a low ebb. Whether the present distribution will continue during years of normal production is a question for the future which only the complex interaction of economic and agricultural factors can decide.

Although there are in existence innumerable types and varieties of popcorn, only five or six are of commercial importance. Until comparatively recently, White Rice, Jap Hulless (Japanese Hulless), and Queen Golden were the chief varieties used. The variety of popcorn called South American, which was introduced some 15 years ago, increased rapidly in favor in the popcorn trade and soon became a serious competitor of the other varieties. The large size of the kernel, its yellow color, and its peculiar "mushrooming" characteristic in popping seemed to catch the public fancy enough so that its toughness and mediocre quality were largely overlooked. An old variety renamed Spanish popcorn was in vogue for a few years, because the large size of its kernels and its ability to withstand processing fitted it admirably for the manufacture of caramel confections. A small-kerneled, smooth, yellow variety of high popping expansion, known variously as Supergold, Sunburst, or Yellow Pearl, also has become of commercial importance. The old Queen Golden corn has now been almost entirely displaced by South American and Supergold, its yellow competitors.

In popcorn the desirable characters to be achieved by the breeder include all of the attributes of a good variety of dent corn, and in addition must include high expansion and tenderness. Fortunately,

high popping expansion and tenderness of the popped kernels seem to be closely correlated, so that in attaining high popability one also is very likely to have a tender product. The absence of a coarse hull and the presence of a good flavor are also desirable characteristics of the final product. Although most people ordinarily do not realize that there are distinctive flavors in various samples of popcorn, these are as characteristic as in different varieties of apples. Some strains have a noticeably sweetish flavor after being popped, some are practically tasteless, while others have a rather strong field-corn flavor.

High expansion in popcorn is dependent upon complete and normal maturity in addition to the inheritance of genes conditioning a dense and elastic endosperm. Since corn diseases usually interfere with normal maturity, it follows that selection for high popping expansion also tends to select for resistance to many of the common corn diseases, such as smut and the stalk and root rots. This is very fortunate for the breeder, since it is, of course, much easier to make improvements in a crop in which desirable characteristics are correlated than in one in which they tend to be mutually exclusive. In the case of popcorn there seems to be a sound basis for placing considerable emphasis on the individual ear-popping test, described later in this article.

METHODS AND RESULTS IN BREEDING

Mass Selection

Of the various methods of corn breeding that have been tried from time to time, that of mass selection alone has stood the test of time as of general application to improvement within open-pollinated varieties of corn without resorting to inbreeding. This is as true of popcorn as of dent corn. Mass selection lends itself particularly to the improvement of popcorn quality. As in field corn, mass selection in popcorn begins with field selection of a large number of ears from desirable plants when the crop is mature but before the first killing frost occurs. These ears should be dried quickly, but not so thoroughly as they would be for seed. About 14-percent moisture gives nearly maximum popping behavior and insures against loss of viability by freezing under any ordinary storage conditions.

After being numbered for identification purposes, the ears can be popped individually by shelling enough from one side of each to fill a small measure for the popping test. After popping, the volume of the product is measured in a suitable container so that the ratio of the volumes before and after popping may be obtained and recorded as the popping expansion. Unfortunately, a standardized method of testing has never been agreed on, so that comparisons of popping tests made by different people sometimes are misleading. In this laboratory ordinary glass graduates are used, as shown in figure 1.

For individual ear tests a popping charge of 25 cubic centimeters ordinarily is measured out in a small graduate, and the popped corn is later measured in a 1,000 cc graduate. Any convenient modification of this procedure that will give an accurate measure of the popping expansion would do just as well. It is highly important, however, that the tests of the various ears be made under as nearly comparable conditions as possible. The factors particularly to be guarded are:

(1) The moisture content of the ears must remain as nearly constant as possible for the duration of the tests, since moisture content has an important influence on popping expansion. (2) The conditions of popping, such as degree of heat used, absence from drafts, etc., should be the same for all tests. (3) A routine procedure in measuring the samples before and after popping should be followed, in order that the same degree of packing may be obtained for every sample.

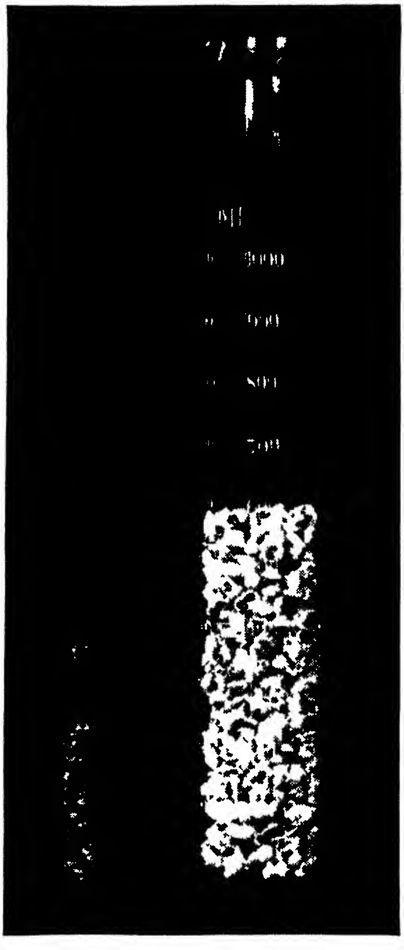

Figure 1.—Glass graduates used to measure the volume of popcorn before and after popping. A popping expansion of about 24 volumes (600÷25) is indicated in this sample.

When samples from a considerable number of ears from an apparently uniform variety are popped separately, striking differences in the popping expansion of the individual ears will be observed. Usually the best ears will show about twice the popping expansion of the poorest ones. The distribution of popping expansion of 1,152 individual ears taken from a small isolated plot in 1928 is shown in figure 2.

By using only the highest 10 or 15 percent of the selected ears for seed purposes a rather rigid selection on the basis of popping expansion can be made. In order to avoid the injurious effects of close breeding in an open-pollinated variety, care must be exercised not to limit too greatly the number of seed ears utilized to propagate the strain. Although it is difficult to set an arbitrary minimum, a mixture from not less than 50 ears should be used to plant the seed plot each year, and one from 100 or more selected ears would be much safer. In following a system of mass selection, the unpopped remnants of the most desirable ears are simply bulked together to furnish seed for an isolated seed plot the following year.

In contrast to the mass-selection method, the pedigree or ear-to-row method may be used, in which each row is planted from a single ear and a preliminary selection is made on the basis of individual rows, followed by selection within the row. It is probable that this method has no advantages over mass selection to counterbalance its disadvantages of more labor and greater likelihood of close breeding.

As in all selection work, there is a constant drag of regression toward the mean of the population in selection for high popping expansion.

Consequently, one may not expect the average popping expansion of the crop produced to be nearly so high as the average of the selected ears that are planted. If the work is carefully and consistently done, however, some progress in raising the mean is accomplished each time, and over a period of years real improvement may be effected, although such improvement may not be expected to continue indefinitely.

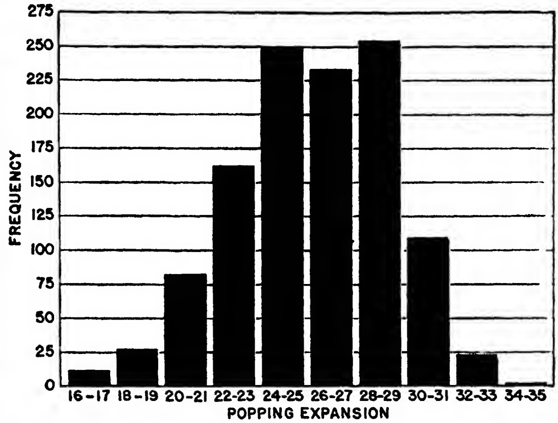

Figure 2.—Distribution of 1,152 individually popped ears of Supergold popcorn harvested from a small breeding plot. Note that the best ears had about twice the popping expansion of the poorest ones.

In an experiment conducted cooperatively by the Department and the Kansas Agricultural Experiment Station to test the efficacy of mass selection in popcorn breeding, the popping expansion was increased from 19 to 26 volumes in 6 years. Comparatively little increase in popping expansion has been effected since that time, which indicates that the practical limits of improvement have about been reached. This work was initiated by J. G. Willier, formerly assistant agronomist in the Bureau of Plant Industry. The resulting improved strain, originally known as Sunburst, but later changed to Supergold, has been distributed by the Kansas station.

Where some attempt at improvement of quality is desired, but where the labor of popping a large number of individual ears for seed selection is out of the question, a modification of the mass-selection method based on kernel structure may be used. A reasonably good correlation ($r = -0.59 \pm 0.022$) has been found [2] between the amount of soft white starch in the center of the kernel and the popping expansion of the ear from which it came. Since the correlation is negative, it means that the ears with the least amount of soft starch in the kernels will on the average pop the best. In selecting seed, three or four kernels from each ear may be split with a sharp knife to determine those with the least amount of soft white starch. These ears should be saved for seed. Although selection for high popability from kernel examination is much less desirable than from direct popping tests, it is much better for the maintenance of a good strain than no selection at all. It is particularly valuable as a means by which to cull out the traces of mixture with dent corn which tend continually to creep into popcorn varieties.

Popcorn Hybrids

Hybridization between inbred lines, the newest and most promising method of corn breeding, is equally as applicable to popcorn as to

[2] Willier, J. G., and Brunson, A. M. factors affecting the popping quality of popcorn. Jour. Agr. Research 35: 615–624, illus. 1927.

dent corn or to sweet corn. A general discussion of corn breeding appears in the 1936 Yearbook of Agriculture,[3] in which the methods and results of hybrid corn production are fully described. With the exception that popping expansion and eating quality must be given paramount consideration in popcorn, the technique followed is the same as for field corn. The possibilities are fully as promising, but thus far comparatively little work has been done in the production of popcorn hybrids.

The only hybrid popcorn known to the writer that has been released for commercial production is Minhybrid 250, from the Minnesota Agricultural Experiment Station. Inbreeding of 200 to 250 lines of Michigan Pop, a selection of Jap Hulless, was begun in 1925 by H. K. Hayes and H. E. Brewbaker. Since 1930 the breeding work has been done by H. K. Hayes and I. J. Johnson. The original lines were culled severely on the basis of agronomic characteristics, so that when the first crosses were made in 1929 only seven remained. These seven inbreds were combined in all possible combinations of single crosses and tested thoroughly during the 4 years 1930–33. On the basis of these trials, single cross C–1 × C–6 was selected as the best combination and named Minhybrid 250. Representative ears of inbreds 1 and 6 and of the single cross are shown in figure 3. The component inbreds were distributed in 1934, and small commercial acreages have been grown in 1935 and 1936. As an average of 3 years' tests at University Farm, Minhybrid 250 has produced 16 percent higher yield and 29 percent higher popping expansion than the standard open-pollinated Jap Hulless used as a check. The adaptation of this hybrid seems to be limited to central Minnesota. In a trial in the southern part of the State the hybrid was much less satisfactory.

In 1931, the Minnesota station also started inbreeding a group of lines from Burbank Pure Gold, a 10-rowed yellow pearl variety. These inbreds are now just ready for top-cross tests and trials of recombination.

At the Iowa Agricultural Experiment Station J. C. Eldredge began inbreeding in 1928 with 50 ears of Jap Hulless, part of which were selected from a mass selection plot of the previous year and part from various commercial growers. These lines have been culled to about 20 inbreds between which combinations have been tested during the period from 1933 to 1936. On the basis of these tests the most promising hybrid seems to be a three-way cross which has averaged about a 20-percent increase in yield and a 20-percent increase in popping expansion over the open-pollinated Jap Hulless used as foundation material. An extensive State-wide test of this hybrid is planned for 1937. No distribution for commercial production has yet been made from Iowa.

In 1933 a new group of inbreds from Jap Hulless, South American, and Supergold were started at the Iowa station, which are still in the developmental stage.

In 1923, J. G. Willier, of the Bureau of Plant Industry, then at Washington, D. C., and later at Manhattan, Kans., in cooperation with the Kansas station, started inbred lines with a yellow pearl popcorn similar to Queen Golden. Later, C. W. Bower, also of this

[3] JENKINS, M. T. CORN IMPROVEMENT. U. S. Dept. Agr. Yearbook 1936: 455–522, illus. 1936.

Bureau, was associated with this work. This investigation was started mainly as an experiment to compare the efficacy of inbreeding compared with mass selection and ear-to-row breeding as a means of popcorn improvement Careful selection was practiced during the inbreeding period, both within and among the inbred lines, for

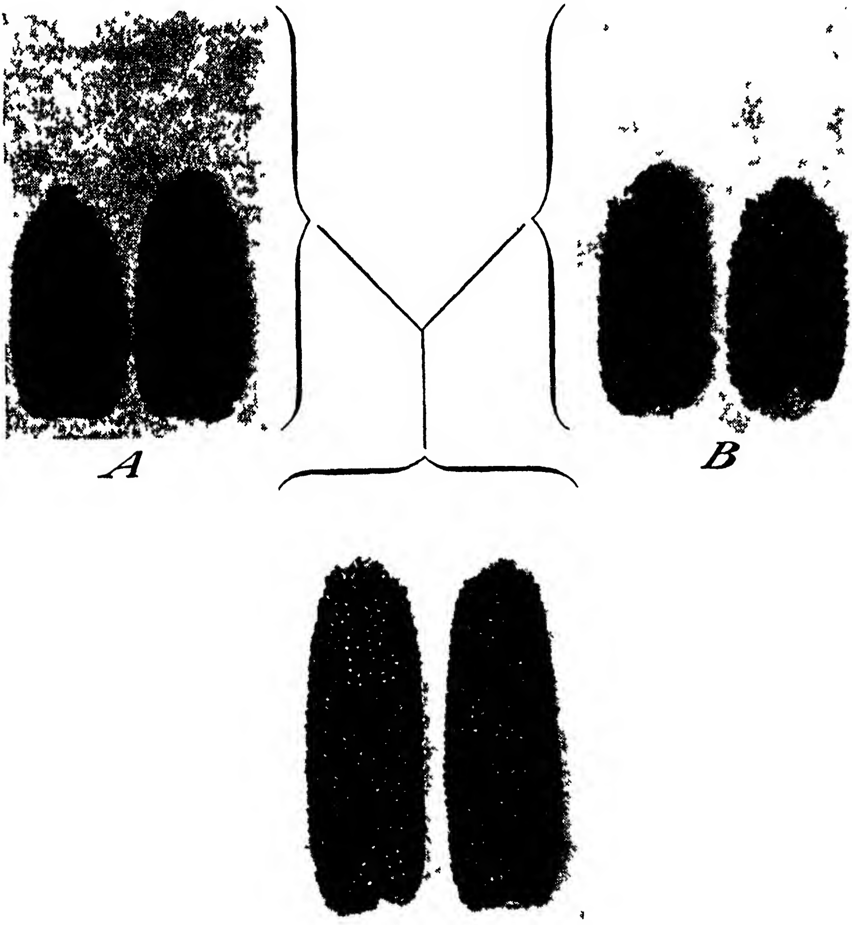

Figure 3.—Representative ears of the two component inbred lines and of the cross in Minhybrid 250· *A*, Line C-1; *B*, line C-6, *C*, Minhybrid 250.

popping behavior as well as for characters of agronomic importance At the conclusion of the work in 1931 it was found that hybrids much superior to the foundation material had been produced During the same period, however, marked improvement in the original variety had been effected by mass selection, as referred to earlier in this article, so that when the mass-selection strain was used as the basis of comparison the hybrids showed no superiority in popping expan-

sion, although somewhat higher yields and considerably greater uniformity of the crop were obtained.

New and much better inbred lines were beginning to be available from the strain already improved by mass selection, so it was decided to drop the original lines and wait until hybrids distinctly superior to existing open-pollinated varieties in popping expansion as well as in yield were available before commercializing them. Preliminary trials of hybrids from this newer material have been very promising, although the corn failures of 1934, 1935, and 1936 at Manhattan have greatly retarded the recent development of the work. In a cooperative field trial near Colfax, Ill., in 1935, 19 of 81 hybrids produced in Kansas had popping expansions of 25.0 volumes or more in comparison with an average popping expansion of 24.1 volumes for the parent stock, Supergold, grown in the same test. The highest popping expansion for any hybrid was 28.5 volumes. Yield was increased even more than popping expansion, the average yield of 72 of the 81 hybrids having uniform stands being 3,218 pounds per acre in comparison with 2,517 pounds per acre as the average of the Supergold checks. Unfortunately, the highest yielding crosses did not also possess the highest popping expansion, but a few were distinctly superior to the parent open-pollinated strain in both respects.

The difficulty of combining top yields and superior popping expansion in the same strain or hybrid of popcorn seems to be a common experience. Apparently the genetic constitution necessary to produce extremely high yields also produces too much soft starch in the centers of the kernels for best popping results. Why this is so is not definitely known. Perhaps the plant is unable, with the plant food materials at hand, to produce more than a given amount of the colloidal matrix in which the starch granules are embedded in the horny portions of the endosperm, and when greater amounts of endosperm are produced, increasing proportions are left in the form of soft starch. If this be the case, the situation is roughly analogous to the difficulty of obtaining a dairy cow with maximum milk production and maximum butterfat content in the same individual. Whatever the causes, it has been the experience of the writer that some compromise must be made in either yield or popping expansion or both to secure the best all-round popcorn hybrids from the utility standpoint.

Less loss of vigor from inbreeding is experienced normally in popcorn than in dent corn. Because of the ability to find comparatively productive inbreds, and because of the small amount of seed required per acre, it probably will be possible to utilize single crosses largely in commercial production. The shape of popcorn kernels from inbreds is about the same as that from their parent varieties, and the size is usually but little smaller, so that no mechanical difficulties with corn planters are encountered in using seed grown on inbred lines in the production of single crosses. The commercial use of single crosses simplifies hybrid seed-production problems and makes possible a most uniform market product.

In the limited trials thus far made, popcorn hybrids between inbreds from different varieties have given the most outstanding increases in yield. This confirms the experience with dent corn hybrids, where crosses between entirely unrelated stocks in the main have been

most successful. Hybrids between inbreds of Supergold and South American have given some extremely high yields, but the tendency toward a negative correlation between yield and popping expansion, referred to above, has seriously limited the usefulness of most individual crosses of this group. A very unusual situation is encountered in crossing South American and Supergold, in that the combination is perfectly fertile when South American is used as the pollen parent, but is almost completely sterile when Supergold is used as the pollen parent. Utilization of hybrids involving this combination must therefore be planned so that Supergold may serve as the seed-producing parent. Demerec[4] reports a similar case of sterility in popcorn, although the varieties involved and the source of material are not clearly stated.

Synthetic Varieties

One variant of the inbreeding method, which has interested corn breeders for some time, is the possibility of recombining a fairly large number of selected inbreds into a synthetic variety that might be better than the original variety and which, because of the number of component lines, could be continued by open pollination without serious reduction of vigor and yield. Starting about 1920 with observational plots and yield tests of all available popcorn varieties, J. R. Duncan, of the Michigan Station, has selected Australian Hulless, Japanese Hulless, Japanese Dwarf Rice, and Queen Golden as the most promising varieties for his conditions and has started inbred lines within these varieties. It is planned to recombine the best inbreds into two synthetic varieties, one within the hull-less group and one within the yellow pearl group. Although in field corn no synthetic variety of outstanding yielding ability has yet been produced, it should be possible, by rigid selection of the inbred lines on the basis of popping expansion, to produce in popcorn a synthetic of high quality. No results of the Michigan experiment are as yet available, but its progress is being watched with interest.

Breeding for Resistance to Diseases and Insects

Resistance to disease is an important consideration in popcorn breeding. Any parasite that saps the vitality of the plant or prevents complete and normal maturity of the grain tends to lower popping expansion. Moreover, the diseases generally grouped as the ear rots are particularly objectionable, since occasional moldy kernels are very undesirable and are practically impossible to separate from corn after it is shelled. The majority of commercial popcorn dealers and processors sort the corn by hand before it is shelled, in an attempt to eliminate diseased ears. Frequently, however, portions of ears with early stages of infection are not easily recognized, and although such corn frequently will pop, it has distinctly undesirable flavors.

No project dealing specifically with breeding for disease resistance in popcorn is known to the writer, although in practically all work, both with open-pollinated varieties and with hybrids, attention is given to freedom from diseases as one of the bases of selection. In the many field-corn hybrids produced experimentally from which the

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[4] Demerec, M. cross sterility in maize. Ztschr Induktive Abstam. u Vererbungslehre 50: 281-291. 1929.

commercial hybrids now in production represent a small and highly selected portion, there has been marked variation in quality. It is likely that just as wide a range of disease resistance will be found in popcorn hybrids. Some of the experimental popcorn hybrids referred to above are very distinctly superior to open-pollinated varieties in freedom from diseases.

Insect damage also is very objectionable in popcorn and is severely discriminated against by the trade. Corn earworms are the cause both of direct damage to the grain and of indirect damage through secondary infestations by other insects and infections with ear rots. Injury by the corn earworm and by storage insects is particularly severe in the Southern States, where it is a serious problem, especially in popcorn, which is used primarily as human food.

At the Texas Agricultural Experiment Station, P. C. Mangelsdorf is attempting to combine the superior resistance of some southern varieties of field corn with the popping ability of popcorn. Of the varieties tried, Yellow Creole has given the most promise of transmitting insect resistance without interfering with popability. By means of a series of crosses, backcrosses, and recombinations coupled with rigid selection, progress is being made and hopes are entertained that a desirable popcorn may result that will be resistant to grain injury by insects.

GENETICS AND CYTOLOGY

THE genetics and cytology of popcorn are the same as for other subspecies of *Zea mays*. These subjects have been discussed in the article already referred to in the 1936 Yearbook of Agriculture,[5] to which attention is directed for detailed information. As a matter of fact, many of the testers used in unraveling the linkage relations in corn have been popcorns or popcorn derivatives. Popping behavior is unquestionably a heritable character, but it is probable that it represents one of the more complex cases of quantitative inheritance conditioned by many genes.

[5] JENKINS, M. T. See *footnote* 3.

BREEDING AND GENETICS IN POTATO IMPROVEMENT

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WHEN the Spaniards invaded South America they found a large number of varieties and species of potatoes under cultivation, the tubers of which were used as a common article of food by the natives. Where these varieties and species originated is not well known, but they seem to be native to the American Continent, since their relatives are still to be found growing wild on the elevated regions extending from the southwestern part of the United States to the southern part of South America, particularly on the higher altitudes in Bolivia and Peru and the coastal regions and nearby islands of southern Chili. All the species seem to require a cool climate, since they are found growing at high latitudes in regions near the Equator and none is known to occur under tropical conditions.

INTRODUCTION INTO EUROPE AND NORTH AMERICA

IF THE origin of the potato is uncertain, its introduction into Europe and North America is also shrouded in mystery. Many interesting legends have been written concerning this, but few reliable facts are available. It is not hard to believe that the Spanish sailors, on their return from their many trips to the New World, brought back potatoes and introduced them into Spain and Portugal. That these were the common potato known today and not the sweetpotato is proved definitely by a report of Clusius published in his Rariorum Plantarum Historia in 1601, giving an illustration and description of a plant sent him in 1588 by the Governor of Mons. The flowers were light purple and the original plant obtained by Clusius produced a fruit ball and two reddish tubers. From Spain and Portugal the potato was taken probably to Italy, from there early in the seventeenth century to Austria, then to Germany, from Germany to Switzerland, and finally to France. The legends surrounding the introduction into Ireland have a more romantic setting. They are centered around Drake, one of Queen Elizabeth's pirates, who was encouraged by the Queen to plunder Spanish ships and Spanish possessions. It is supposed that on one of these trips Drake obtained potatoes in the West Indies for his ship's stores and that some of these were carried to Ireland about 1586.

Little is known of the introduction of the potato into North America. It is generally believed that the English colonists of Virginia and Carolina obtained the potato from Spaniards or from other travelers. The most authentic report shows that potatoes were first grown in this country at Londonderry, N. H., in 1719, from stock brought from

Ireland. It was for this reason, no doubt, that the potato was called the "Irish" potato. The name is still used, especially in the South, where it serves to distinguish the potato from the sweetpotato.

Most of the stories of the introduction of the potato into Europe and North America are no doubt legendary, as well as some of the tricks that were supposed to have been adopted to get people to use the tubers for food. The spectacular increase of the potato as a food crop, however, is not legendary, but is one of the miracles of agriculture. Although it is only a little over 300 years since the first introduction into Europe and about 200 years since the first importation into the United States from Ireland, the potato is now grown in almost every important agricultural country in the world. The crop for the United States and Canada for 1934–35 was nearly half a billion bushels, and the total for the world, not including the Union of Soviet Socialist Republics and China, for which no data are available, had reached the stupendous figure of over 6 billion bushels.

BOTANICAL RELATIONSHIPS

THE potato belongs botanically to the section *Tuberarium* (*50*)[1] of the genus *Solanum*, the members of which are, with few exceptions, tuber bearing. This section comprises not only the cultivated forms but many wild species. Since it is probable that undiscovered species occur in regions not yet explored by botanists, the total number cannot be definitely stated, but it is believed to exceed 100.

[1] Italic numbers in parentheses refer to Literature Cited, p. 434.

MILLIONS *of dollars are spent each year in providing ways and means of protecting the potato crop from diseases, and these colossal efforts have done their part in providing the consumer with potatoes fit for consumption; but in spite of them, many millions of bushels are lost each year. The annual loss from late blight alone has averaged 9,000,000 bushels for the past 10 years. Thus disease resistance has been a major objective in the well coordinated national potato-breeding program now being conducted throughout the United States, in which the Department of Agriculture and all interested States closely cooperate. Already many varieties have been obtained resistant to late blight, to scab, and to two of the mosaic diseases. The results indicate that by using genetic principles as a working tool, it should be possible to solve many if not all of the disease problems of potato growers by combining resistance with superior qualities of economic importance, such as shallowness of eye, desirable shape, good cooking quality, high yield, and adaptability to local conditions.*

Considerable confusion has existed in the past in regard to what has been considered the species *Solanum tuberosum* L., which has generally been understood to comprise all cultivated varieties of potato. These have recently been assigned by Bukasov (*9*) to 14 species. According to his classification, *S. tuberosum* includes the Chilean cultivated forms as well as the commercial varieties of North America and Europe, which he believes to be of Chilean origin. Most of the common cultivated varieties of the Andes region are placed in the species *S. andigenum* Juz. and Buk. The 12 remaining species are grown in small local areas in the Andean countries and more or less resemble the wild species in their general appearance. It is doubtful whether any of the cultivated varieties of Europe and North America as known today have been derived from them.

EARLY IMPROVEMENT IN THE POTATO

There is little information available regarding the source of the potato stock grown during the first 100 years after its introduction into the United States. It is believed that not many new varieties of importance were produced during that period. During the second century of potato culture in this country, however, there was great activity in the production of new varieties. Data reported on 228 of these varieties show that they originated in 21 States. New York and Vermont, however, produced 50 percent of the total number. Of the 160 varieties whose date of origin is known, 80 percent were produced during the 40-year period 1861 to 1900 and 48 percent during the two decades 1871 to 1890 (*12*).

The most important varieties produced during this 100-year period and their originators, as reported by Stuart (*71*), are given in the appendix.

Special mention should be made of C. E. Goodrich, as his work was the first to produce lasting results. He believed that the disastrous epidemics of late blight during the years 1843–47 were the result of a reduction in the vigor of the plants caused by long-continued propagation by vegetative means and that this vigor could be restored by growing plants from true seed. While he did not succeed in the control of late blight by this means, he may be considered to have laid the foundation of potato breeding in this country by furnishing material to be used by other breeders. The ancestry of 170 varieties can be traced back to Goodrich's Garnet Chili, a seedling of the imported Rough Purple Chili. They include several of the well-known varieties of commerce, such as Beauty of Hebron, Burbank, Early Ohio, Early Rose, Green Mountain, Prolific, and Triumph.

The work of Pringle, as recorded by Stuart (*71*), is outstanding in that it represents what is believed to be the first systematic effort to obtain seed by controlled hybridization. This seed was not only used for the production of the varieties he introduced but was disseminated to others through his contract with a seedsman in New York to furnish hybridized seed at $1,000 a pound.

Many varieties of excellent quality and high yielding ability, which were the principal objectives, were produced during this period. The work, which made important contributions to the agriculture of this

country, was carried on entirely by private agencies rather than by public institutions. Most of the men engaged in the early work were practical potato growers, except C. E. Goodrich, who was a clergyman, of Utica, N. Y., and E. S. Carman, who was editor of the Rural New Yorker.

PRESENT-DAY PROBLEMS

The commonly grown commercial varieties of potatoes differ from one another in earliness, tuber shape, adaptation, depth of eye, cooking quality, and yielding ability. In certain of these characters, such as yielding ability, some of these varieties have reached a high standard of excellence when grown under conditions to which they are adapted. These same varieties are, however, poor in other characters. Some are not adapted to a wide range of conditions; others have deep-eyed tubers, which cause waste in preparing the potatoes for cooking. All are susceptible to one or more of the common potato diseases, including the virus diseases, late blight, common scab, fusarium wilt, rhizoctonia, early blight, and blackleg. Control of these diseases requires a continual fight on the part of the potato grower and adds greatly to the cost of producing the crop.

The group of diseases caused by viruses are perhaps the most widespread and the most baffling. In this group are found mild mosaic, latent mosaic, leaf roll, spindle tuber, and yellow dwarf. These diseases occur in every potato-growing region of the United States, and it is probable that not a single field could be found entirely free from them. They are not new. Their effects have been observed by growers for many years, but for a long time it was thought that they were due to "running out" or "degeneracy", brought about by growing potatoes year after year from the same tuber stock. It is only a few years since it was discovered that these troubles are due to virus diseases. It was soon observed that some varieties did not "run out" so quickly as others, or, as we now say, some varieties are more resistant to the attacks of certain viruses than others. Knowing that such differences must have a genetic basis, breeders are working to obtain resistance to these diseases in combination with other characters of economic importance.

Late blight, caused by *Phytophthora infestans* (Mont.) DBy., adds more to the cost of producing the potato crop than perhaps any of the other diseases. The losses from this disease alone have been more than 9 million bushels a year for a period of 10 years, according to estimates issued by the Division of Mycology and Disease Survey, Bureau of Plant Industry, United States Department of Agriculture. In some seasons and in certain localities the disease causes very little damage. At other times (as in 1927, 1928, 1932, and again in 1936) large losses are sustained by growers. The heaviest loss for any one year, nearly 31 million bushels, was reported in 1928. That year late blight was reported in 15 States, with the loss in New York estimated at approximately 13 million bushels. In 1932 the reduction of the crop was estimated at 9,230,000 bushels, the greater part of which, 9,058,000 bushels, was reported from Maine. Again in 1936 heavy losses occurred in Maine.

It is true that late blight can be controlled to a large extent by careful spraying with bordeaux mixture, but despite the fact that

control measures are being practiced more generally than ever and that spray equipment has been improved and spray programs have been more faithfully carried out, large losses continue to occur, not only from reduction in yields but also from interference with marketing operations. Rot may develop on infected tubers in storage and in transit. Because of the uncertainty involved, the buyer is reluctant to purchase potatoes for storage purposes. There is considerable expense every time a carload is regraded at a terminal market, and this happens frequently in blight years. These losses all affect the grower.

Common scab, caused by *Actinomyces scabies* (Thax.) Gues., is another disease that takes a toll from the grower. The organism causing this disease lives over in the soil and is also carried on the tubers. Treatments have been recommended that will kill the organisms on the tuber, but no one has yet devised a method to fully protect the growing tubers from the soil-borne organisms.

Millions of dollars are spent each year in providing ways and means of protecting the crop from the attacks of these and other diseases, but comparatively little attention has been paid to obtaining varieties resistant to the attacks. The colossal efforts in the way of plant protection have done their part in providing the consumer with potatoes fit for human consumption, but in spite of these efforts millions of bushels of potatoes are lost each year. Results already obtained indicate that by using genetic principles as a working tool it should be possible to solve many if not all of these problems by producing new varieties in which resistance to various diseases is combined with other characters of economic importance, such as shallowness of eye, desirable shape, good cooking quality, and high yield.

In the production of such varieties the plant breeder must be familiar with the local problems of growers; he must have a knowledge of the existing varieties and the important economic characters of each; and he must be familiar with the botanical structure and behavior of the various parts of the growing plants. A knowledge of the modes of reproduction with the advantages and limitations of each is the first essential.

REPRODUCTION IN THE POTATO

The potato plant is reproduced in two ways. In commercial practice it is grown from tubers, a method of vegetative or asexual reproduction. Plants can be grown from true seed, however, by sexual reproduction.

Asexual Reproduction

A number of mutations in the vegetative cells of potatoes have been studied and described, but they are too few and far between to be relied upon in a breeding program as the only source of variation. In many cases, too, the changes are of minor importance. Clark (*13*) has described several mutations that have occurred in the color of the skin and of the eyes. Salaman (*57*) classifies mutations of this sort according to whether they are due to the acquisition or to the loss of a character and whether they affect the tuber only or the whole plant. Mutations due to the loss of a character are by far the most common. There are a number of instances where the red tuber loses part of its

color and becomes "splashed", or loses all of its color and becomes white. Purple tubers may become red, purple splashed, or white. Somewhat similar changes have been observed for flower color. Mutations due to the acquisition of a character, which might be called positive mutations, are much rarer. Examples are a red-tubered sport from a white-tubered variety, or a fully colored one from a partially colored variety. Mutations occurring in more than one character in the same individual are extremely rare. Mackelvie (*38*) reports such a case in which there was a white-tubered mutation combined with a different leaf shape from that of the parent variety. The

Figure 1.—Potato plants grown from true seed in the greenhouse. These plants have been transplanted from the germination pots to individual pots where they will be grown until they are transplanted in the field.

leaflets of the mutant were narrower and more pointed. The yield was reduced also.

East (*22*) carried out some rather carefully controlled studies on the occurrence of somatic or vegetative mutations in the potato. In these studies each variety was started from a single hill. During the course of the study five permanent changes from pink to white tubers, two permanent changes from long to round tubers, and four instances of changes from shallow to deep eyes were observed. Selection for high nitrogen content gave negative results.

Clark (*16*) made a study of six commercial varieties to determine whether their origin could be accounted for by mutation. The methods employed were those reported by Asseyeva (*1*) for this purpose. They consisted of removing from the eyes of the seed pieces

the outer layers of tissues, which, in skin-color mutations, are the mutating tissues. This allowed the sprouts from which the plants under test were grown to develop from the deeper layers, the original unchanged tissue. Clark found that four of the varieties studied were mutations in the outer layers of the tuber. Two were mutations from smooth skin to russet skin, the third was a mutation from colored to colorless skin, and the fourth from colorless to colored skin.

That the occurrence of such mutations has not been an important factor in the development of potato varieties is shown by Clark (*12*), who reported that of 380 varieties that have originated in the United States and have at one time or another been introduced to the commercial trade, 306, or 93.3 percent, were of seedling origin, and only 22, or 6.7 percent, were reported as so-called sports or mutants. Of the 22 varieties reported as sports, 4 are white-tubered from varieties with colored tubers, and 4 are late-maturing variations found in early varieties. The meager information regarding the other 14 furnishes no basis for determining whether they were actual mutations or mixtures carried in the seed stock or volunteers that had persisted in the soil from some preceding crop.

Even if only a few varieties have arisen as the result of somatic mutations, they are still a source of variation that cannot be ignored entirely by the breeder.

Since it is quite impracticable for the plant breeder to make much improvement by selecting tubers of a variety with the hope of getting something new, he has to resort to the use of seed as a means of inducing variations.

Sexual Reproduction

As has been shown by Clark (*12*), most of the varieties that have originated in the United States were produced by growing plants from true seed (fig. 1). Salaman (*55*), discussing the production of new varieties from the same source in England, states: "It is by this method that practically every variety which has ever been raised since the introduction of the potato in 1588 has been attained."

True seed is a product of sexual reproduction and is found in the fruit or ball, which is quite similar to a small tomato (fig. 2). Under certain conditions these fruits are produced in abundance on some varieties but are rarely if ever seen on others. They are the result of the maturing of the flower, and each of them may contain 200 seeds or more.

The flower of the potato is what is known to botanists as a complete flower with calyx, corolla, stamens, and pistil. There are usually five stamens surrounding the pistil. The process of pollination is very simple because of the simple structure of the flower parts. Pollen may be brought to the stigma of the pistil in several ways. In varieties in which the pistil is the same length as the stamens or shorter, the mature anthers may come in direct contact with the stigma. When the pistil is longer than the anthers, pollen may fall upon it when the flower droops over, as it frequently does at the end of the day. Insects may be responsible for a much greater amount of cross-pollination than is commonly supposed; in some localities bumblebees and honeybees are often seen visiting potato flowers. Pollination may be effected also by the manipulations of the plant breeder.

The technique of cross-pollinating potatoes by hand is comparatively simple, but since relatively few varieties produce viable pollen, the setting of seed is often very small in amount. If a variety producing viable pollen is used as the female parent, the flower must be emasculated, that is, the anthers must be removed. This must be done before the anthers are mature, or the flower will be self-pollinated. Generally speaking, the anthers should be removed before the pistil protrudes through the bud, or a day or two in advance of the opening of the flower. A pair of sharp-pointed forceps is the only instrument necessary. All the flowers in the cluster that are in the right stage of maturity are emasculated, all others are removed, and the inflorescence is enclosed in a 1-pound paper bag, which is securely tied on. If the variety used as the female parent does not produce viable pollen, it is not necessary to emasculate before pollinating.

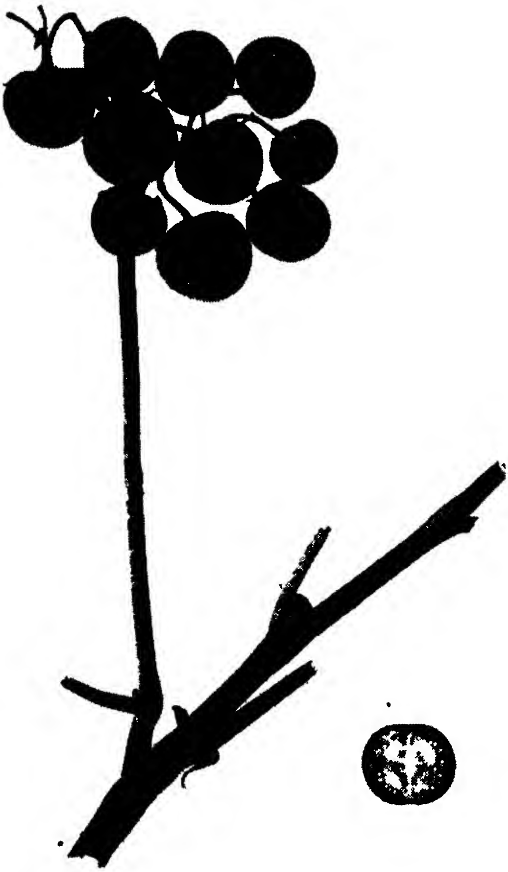

Figure 2.—Potato seed balls, the result of natural pollination of a variety that produces fertile pollen.

In pollinating, flowers with anthers ready to open are obtained from the male parent. These are placed on the thumbnail and the anthers are tapped gently with the forceps. The stigma of a seed parent is then gently rubbed in the pollen on the thumbnail until it is completely covered (fig. 3). The treated flowers are covered with the paper bag again. It has been found best to enclose as much foliage with the flowers as possible, to protect them from injury and to supply moisture; otherwise the flowers may dry up and fall off. The failure or success of the fertilization can be determined within a week or 10 days (fig. 4). As soon as the seed balls develop, the paper bags are removed and replaced by a cheesecloth sack, which is tied securely to the vines

Every breeding method has its advantages and limitations, and which one or which combination is used depends to a large extent on the problem involved in a particular case. The potato breeder today uses (1) the introduction of new varieties or species, (2) selection of clonal lines, (3) varietal crossing, (4) sib mating (brother-sister mating), (5) backcrossing to parental lines, (6) selfing and recombining selfed lines, (7) outcrossing to unrelated lines, (8) strain building, and (9) crossing of different species.

Since a discussion of these steps and methods involves a number of rather technical points, it will be postponed until later in this article,

Figure 3.—Pollinating potato flowers.

after the work now being done in potato breeding in the United States has been outlined.

THE NATIONAL POTATO-BREEDING PROGRAM

Because of the effect of environment on the fruitfulness (seed production) of potato plants, it is difficult, if not impossible, for many of the State experiment stations interested in some aspect of potato-breeding work to produce true seed. This would prevent the application of genetic principles to breeding problems and close the most promising avenue for their solution. Certain Northern States and other States with mountainous regions where potatoes can be grown at high elevations are especially favored, since true seed of many strains and varieties, as well as tubers of good quality, relatively free

from disease, can be produced in such places. In potato breeding, then, more perhaps than in any other breeding project, it is necessary that the interested States cooperate in their attacks on the many problems involved.

Organization of the Work

Since problems and objectives in potato breeding often cut across State lines and involve large regions of the entire country, the breeding work has been organized as a national project with all the interested State experiment stations and the United States Department of Agriculture cooperating. A number of the cooperating stations are

Figure 4.—Seed balls 8 days after the pollination operation shown in figure 3. These fruits are the source of seeds from which new varieties are produced.

now carrying on complete breeding programs—that is, they are able to produce true seed and raise seedling progenies for genetic analysis of the material they are interested in, and at the same time to produce improved varieties. The States of Minnesota, North Dakota, Michigan, New York, Louisiana, and North Carolina and the Department working in Maine and Colorado are at present producing true seed. If any of these find they can use more seed than they are able to produce, a supplementary supply is sent from Maine, Minnesota, or Colorado, or from any other State that has a surplus. True seed is also sent to other States not able to produce their own, such as Iowa, and in 1936, Nebraska and Wisconsin. The last two States have recently undertaken complete potato-breeding programs.

A number of States that do not grow potato seedlings test the most promising seedling varieties produced by others. New introductions,

parent material, and tubers representing seedling progenies are distributed to any State experiment station that can make use of them. The Department has been active in the production and distribution of such material and by common consent of the cooperators has been designated as the coordinator and clearing house for the project as a whole. A brief outline of the work carried on at the various stations under this project follows.

For a number of years the Department workers have been carrying on an intensive program of potato breeding at Presque Isle, Maine, in cooperation with the Maine Agricultural Experiment Station. As a part of the national potato-breeding program they are now engaged in (1) the production of true seed for use at Presque Isle and for distribution to other cooperating experiment stations; (2) distribution of single-tuber selections of various progenies to cooperating stations; (3) distribution of named and numbered seedlings for tests at other stations; (4) yield trials; (5) disease-resistance tests, including resistance to mild mosaic, latent mosaic, spindle tuber, leaf roll, late blight, and common scab; (6) genetic and cytological studies; and (7) the production of early-maturing varieties. In all this work higher market and cooking quality are being considered.

The work at the United States Horticultural Station, National Agricultural Research Center, Beltsville, Md., is interwoven with that carried on at Presque Isle and at other stations included in the national potato-breeding program. Two of the important aspects of the work at this station are the production of seedlings and the testing of seedling progenies and parents for resistance to virus diseases such as mild mosaic, latent mosaic, leaf roll, and spindle tuber. Tests are also made in the greenhouse for resistance to late blight and to the attacks of *Fusarium eumartii* Carp. and in the field for resistance to *F. oxysporum* Schl. Resistance to blackleg is being studied in certain progenies.

Iowa produces seedling progenies from seed furnished from Maine and Minnesota and tests the promising material produced by other cooperating States for its adaptability to Iowa conditions.

Louisiana produces some of the seed used in the production of seedling progenies. Other seed and material are supplied by Minnesota and the Department. Resistance to various diseases and adaptability of potato varieties to southern conditions are being emphasized.

The work in Michigan consists of growing seedling progenies, testing Department seedlings and those produced by other cooperating stations, increasing new varieties, carrying on disease-resistance studies with special reference to yellow dwarf and common scab, and producing early varieties with better market and table quality and varieties more suitable for muck soils.

In Minnesota securing resistance to virus diseases and to common scab in combination with early maturity is the main problem. A study of inbreeding and the recombinations of inbred lines is being carried on, and also a study of the cytological behavior of species hybrids.

In New York (Cornell University) resistance to late blight, using an immune wild species as the parent from which to obtain resistance, is one of the objects of the breeding work. Tests for resistance

to streak and leaf roll are being conducted. A much enlarged program is just now getting under way, which will emphasize market quality, cooking quality, adaptability, and resistance to a number of diseases other than late blight.

In North Carolina the work consists of the production and testing of seedling progenies produced at Raleigh and the testing of the most promising material grown at other stations. The emphasis is being placed on earliness and on resistance to disease and to leafhopper injury.

North Dakota produces some true seed but is supplied for the most part from Presque Isle, Maine. Varieties as early as Irish Cobbler but smoother and higher yielding are being sought.

The Department workers at Greeley, Colo., are attacking the problems of resistance to wilt, to psyllid yellows, and to common scab in relation to other characters of economic importance.

In Nebraska potato-breeding work has only recently been started. Earliness, yield, quality, and resistance to diseases will be emphasized. To begin with, resistance to fusaria is being studied.

In Wisconsin a complete breeding program has recently been undertaken. Studies of the breeding behavior of resistance to common scab and virus diseases, as well as of other characters of commercial importance, are getting under way.

In Charleston, S. C., at the United States Regional Vegetable Breeding Laboratory, breeding work recently initiated will deal with the problems of potato production in the coastal region of the Southern States, which center around yield, earliness, and drought resistance.

In Pennsylvania, at Drifton, a test project for potato wart resistance is conducted by the State Department of Agriculture in cooperation with the United States Department of Agriculture. A number of the most promising named and numbered seedling varieties are tested for resistance to this disease each year in soil infested with organisms that cause the wart disease.

In Florida, at Hastings, the Florida Agricultural Experiment Station has begun the study of resistance to brown rot in the potato in cooperation with the Department. A few varieties and seedlings have already been tested, and the experiment will be greatly enlarged in 1937.

In Indiana, Purdue University has recently initiated a program of breeding for disease resistance as a part of the national potato-breeding program.

In addition to the special problems enumerated above, the following States are cooperating to determine the adaptability of the new named and numbered seedling varieties produced by the Department or by any of the State experiment stations: California, Connecticut, Florida, Indiana, Iowa, Kansas, Louisiana, Maryland, Massachusetts, Minnesota, Michigan, New Hampshire, New Jersey, New York, North Carolina, North Dakota, Ohio, Oregon, Rhode Island, South Dakota, Tennessee, Virginia, Washington, and Wisconsin.

The cooperative potato-breeding work has not stopped at national boundaries, for material has been exchanged with a number of workers in Canada and other foreign countries.

Recent Results with Various Methods of Breeding

Clonal Selection

Progress has been made by the use of clonal selection in the State of New York. According to a recent unpublished report by J. R. Livermore, one of the cooperators in the national potato-breeding program, this method has been employed in connection with potato improvement work at Cornell University in cooperation with growers since 1905. Four varieties have been selected from the Smooth Rural (Rural New Yorker No. 2) and named. These are Heavyweight, No. 9, Pioneer Rural, and Toanco 4. A strain of Irish Cobbler has been named Pioneer Cobbler. Many other high-yielding clonal lines have also been selected from commercial varieties and are being produced by various growers. White-skinned bud sports from russet stock, the plant tops exhibiting heat resistance and the rugged vigor of the Russet Rural, have also been found. The Red Warba, one of the varieties recently introduced by the Minnesota Agricultural Experiment Station, occurred as a bud mutation from the Warba. This might be considered a clonal selection. By the method of careful selection within a variety or clon, not only are mutations uncovered but disease-free material is obtained, which in itself is justification for careful observation and selection.

Inbreeding and Recombination of Selfed Lines, Etc.

F. A. Krantz, of the University of Minnesota, another of the cooperators in the national potato-breeding program, has been placing greater emphasis than other breeders on the method of selection in selfed lines and recombinations between them. The results have been very similar to those found by the corn breeders, that is, selfed lines become homozygous and are less vigorous than the parent stocks from which they originated. Certain undesirable characters have segregated and been eliminated, such as short internodes, prostrate plants, simple-leaved types, chlorophyll deficiencies, and tuber abnormalities. Most important from the breeding standpoint, a number of self-fertile lines carrying desirable characters have been selected. In a brief unpublished summary of results to date, Krantz says:

> Selection in self-fertilized lines has been effective in establishing pollen fertility in combination with a wide variety of other characters. Used in combination with outcrossing it has facilitated the development of a large body of seed-setting material possessing selected germ plasm of the common varieties.
>
> The results show that it will be possible through this method gradually to combine the best germ plasm in the potato into a useful form for breeding purposes. The difficulties involved are the absence of information on the best selection technique and the necessity of developing one suitable for effectively selecting and combining desired characters. Pollen sterility at the outset also presented a serious problem since selection was restricted to the seed setting individuals. The difficulties mentioned are associated with potato breeding in general and are not specific to any particular method. Information is gradually accumulating on methods and technique of selection in inbred lines. The difficulty of maintaining and continuing inbred lines has been greatly reduced through selection for high fertility. Comparisons have been made and are in progress of varietal crosses, single crosses, three-way crosses, and top crosses to determine the relative hybrid vigor that might be expected from the different types of combinations. The inbred lines are valuable for their concentration of desirable characters in combination with pollen fertility, early maturity, upright sturdy vines, resistance to certain virus diseases, fine cooking quality, and varying rest periods.

Species Hybridization as a Method of Obtaining Late Blight Resistance and Frost Tolerance

Most of the attempts to produce blight-immune varieties of commercial value by the use of species hybrids have resulted in failure. Recently, however, Donald Reddick, of Cornell University, also a cooperator in the national potato-breeding program, has been getting promising results from such hybrids. For a number of years it had been known that certain forms of *Solanum demissum* Lindl. were immune to late blight. In 1928 Reddick began using hybrids between these and cultivated varieties in an attempt to combine this immunity with characters of the cultivated forms. Two years later the Department sent Reddick and three men from the Division of Plant Exploration and Introduction, C. O. Erlanson, Paul Russell, and M. J. Souviron, on an expedition to Mexico to find, if possible, more sorts of potatoes, either wild or cultivated, that might be resistant to this disease. A large number of collections were made. Among these several varieties of *S. demissum* were found to be immune and to have at the same time some frost tolerance.

In commenting on the methods and some of the difficulties that arise in this work, Reddick says:

> The object has been to get the blight immunity and frost tolerance of a wild plant into a plant of commercial value. Owing to sterility, incompatability, etc., the results thus far have been simply what could be got, not what it was planned to get. Efforts have been made from the beginning to determine the mode of inheritance of blight immunity and frost tolerance, but inability to obtain sets of seeds of the kind desired has prevented determining the mode. The original crosses are interspecific and involve hybridizing 72-chromosome plants with those having 48 chromosomes. Practically all of the crosses have had to be 48 male to 72 female, because the reciprocal cannot be effected. The second generation of such crosses does not segregate but "reverts" to the wild type. Repeated backcrossing eliminates most of the wild characters but blight immunity is transmitted.

This work has been in progress since 1928. Some of the families are progenies resulting from an original species hybrid between an immune species and a cultivated variety that has been backcrossed to cultivated varieties four successive times. Fifty percent of the progeny of the fourth backcross are immune to the late blight disease. As a result of this work Reddick has at the present time about 500 families of plants immune to late blight. Possibly 50 or more of these are approaching the commercial ideal as to size, color, shallowness of eye, heat tolerance, and date of maturity. They are still to be tested for yield, quality, and adaptability to various localities. A few of these families will stand at least four degrees of frost.

Results in Relation to Disease Resistance

Resistance to Virus Diseases

The potato breeders and pathologists of the Department, using the methods included in strain building (p. 429), are making real progress, both from the standpoint of scientific knowledge and of practical results in breeding for resistance to virus diseases. One variety produced, U. S. D. A. seedling 41956, is highly resistant if not immune to the virus of latent mosaic. It has been exposed to the disease in the field by being grown near other varieties known to have this

disease, and diseased stocks of other varieties have been grafted on the stems and on the tubers, but so far it has withstood every attack. A number of the progeny of a cross in which this variety was used as one of the parents show the same character, which indicates that immunity to latent mosaic is heritable. A number of other seedling varieties are resistant to this same virus in the field-exposure tests but contract the disease in tuber-graft tests, where it is expressed as top necrosis or death of the top of the plant. On the other hand, several attempts have been made to find even a single plant of Green Mountain free from this disease, but up to the present time such attempts have resulted in failure.

A large number of seedling varieties are highly resistant in the field tests to another virus disease, mild mosaic, perhaps the commonest of the "running out" diseases. These varieties have all contracted the disease, however, in the more severe tests of tuber grafting. In comparison with these resistant types, Green Mountain has been known to become 100-percent diseased with mild mosaic in the field exposure tests within a period of 3 years.

The fact that two virus diseases can be controlled by the production of resistant varieties gives hope that other virus diseases, such as spindle tuber and leaf roll, can be controlled in a similar manner. Comprehensive field-exposure and tuber-graft tests of a large number of seedlings and varieties are being made at the present time to determine whether any of them are resistant to either of these latter diseases. So far the results have not been encouraging. Although there have been a few escapes in the field-exposure tests, it is quite possible that none of the varieties so far tested is resistant to either of these diseases. Some of them may carry recessive factors for resistance, however, and many of them will be analyzed genetically to determine whether this is the case, and if it is, efforts will be made to combine the resistance with other characters of importance to the grower. In the case of leaf roll, a few recent introductions are reported to be resistant and will be used in future work. At the same time, the search in the United States and in foreign countries will be continued until types resistant to every virus disease are obtained or until all the possibilities for finding resistance are completely exhausted.

Resistance to Late Blight, Derived from Cultivated Varieties

Breeding for resistance to late blight was begun at a comparatively early date. In 1870 Darwin attempted through the use of species hybrids to produce varieties resistant to *Phytophthora*, but was evidently not successful. According to Stuart (*71*), the first American breeder to attempt the control of late blight by the introduction and production of blight-resistant varieties was Chauncey Goodrich, of Utica, N. Y., whose work has already been mentioned. This work was based on a small quantity of South American potatoes that he received in 1851 through the American consul at Panama. A number of other breeders made valuable contributions during the latter part of the nineteenth century, but with the exception of the work of Goodrich, resistance to late blight seems not to have been emphasized in the United States until potato breeding was actively undertaken by the Department in 1910.

According to Clark et al. (*18*), the only disease resistance sought at the time was to the late blight fungus. This work had not progressed very far, however, when it became evident that the virus diseases had to be given the chief consideration, and it was not until the present national potato-breeding program was under way that emphasis could be placed once more on breeding for resistance to late blight. Reddick, working in cooperation with the Department, had already undertaken the solution of this problem, using species hybrids. The Federal work at Presque Isle, Maine, and Beltsville, Md., includes the genetic analysis of the cultivated varieties to determine the possible existence of blight-resistant factors.

In 1932, when late blight caused the loss of over 9 million bushels of potatoes in Maine, 700 seedlings, representing 4 different progenies, and about 100 Green Mountain checks, were grown at Presque Isle in test rows of from 20 to 30 hills each. This plot, about 1½ acres in area, was not sprayed with bordeaux mixture but was sprayed in July with a single application of calcium arsenate to kill the Colorado potato beetle. Late blight infection was first observed on July 22. Conditions favorable for the spread of the disease prevailed during August, so that by the first week in September nearly all the seedlings and all the Green Mountain checks were completely killed, both leaves and stems. A few seedlings had stems and about one-fifth of the leaves remained free from blight infection, and a still smaller group had only a few infected leaves. There were no seedlings completely free from the disease. A number of the most resistant lines were found in a progeny of Katahdin, naturally fertilized. A few seedlings of the cross Chippewa × Katahdin, both of which are susceptible to blight, escaped with very little injury. From this test it was evident that there are different degrees of resistance; that resistant varieties can be obtained by inbreeding certain susceptible varieties and by crossing two susceptibles. The test showed also that lateness is not completely correlated with blight resistance or escape, since all the seedlings were comparatively late, but hundreds of them were killed by blight before they had time to mature.

Since 1932 a large number of varieties and seedlings have been tested for resistance, some of them at Presque Isle, Maine, and some in the greenhouse at Beltsville, Md., under conditions favoring heavy infection. At Presque Isle blight spores are sprayed on the plants under test on evenings preferably cool and damp. In the greenhouse steam is turned into the section in which the plants are being tested, to produce a high humidity, and the plants are then sprayed with spores of the fungus. Heavy epidemics are usually induced by these methods, and unless a variety is resistant, there is little chance of escape. A number of introductions from Germany and elsewhere, as well as a comparatively large number of progenies, have been put through these tests during the last 4 years. The results obtained with some of these were reported by Stevenson et al. (*67*) and need not be repeated here. It should be said, however, that there are now available hundreds of varieties and seedlings showing varying degrees of resistance to late blight. A few produced from seed received from K. O. Müller, Berlin-Dahlem, Germany, have completely escaped infection, even under epidemic conditions such as prevailed in the Presque Isle tests in 1936.

From the commercial standpoint one of the most promising selections up to the present time is from a cross of Chippewa × Katahdin. This variety came through the epidemic of 1932, unsprayed with bordeaux mixture throughout the growing season, with very slight injury. It has been included in the greenhouse tests at Beltsville and again in the field at Presque Isle in 1936 and produces a good crop, even when sprayed with blight spores. It has yielded slightly more than Green Mountain for an aveiage of 5 years at Presque Isle and has good cooking quality when grown at Aroostook Farm. Other promising seedlings highly resistant to blight are from a cross between No Blight and Katahdin. No Blight is described by Bonde (*6*) under the name Foster Rustproof, and Katahdin has been described by Clark et al. (*18*). No Blight is quite resistant to late blight. Katahdin is susceptible, but it carries a factor or factors for resistance in a heterozygous condition, as is shown by the fact that blight-resistant seedlings have been found in a progeny of Katahdin selfed. Some of the blight-resistant seedlings from the cross No Blight × Katahdin are being tested for yield and other characters. Two years' tests show them to be in about the same class as Green Mountain with respect to yield. Another cross from which a number of promising selections have been made had for parents Ekishirazu, a Japanese variety, and seedling 45349, the latter a seedling of Katahdin open-pollinated. Seedling 45349 was selected in 1932 and has shown a fair degree of resistance in a number of tests since that time.

Figure 5 shows the difference between the appearance of the vines of a resistant seedling on which very little late blight developed and the Green Mountain check, which was completely killed by the disease. Both of these were sprayed with blight spores to induce the epidemic.

The tubers of a number of the seedling varieties are resistant to tuber rot caused by the late blight fungus. Reiner Bonde, of the Maine Agricultural Experiment Station, has tested a number of them by putting blight spores on the surface of the tubers and then placing them in a moist chamber in a temperature conducive to development of rot. A number of the seedling varieties remained free from rot except where the skin was broken. The Green Mountain check rotted completely in a very short time (fig. 6). Many varieties therefore have been produced within the last few years by hybridization and selection that are resistant enough to late blight to be grown successfully without being sprayed even in years when this disease occurs in epidemic proportions. Several of these are promising also from the standpoint of other characters of commercial importance.

Resistance to Common Scab

Another disease that takes its toll wherever potatoes are produced is the common scab caused by *Actinomyces scabies*. Scab is not so noticeable in its effects on yields as is late blight, but it affects the market quality and hence the value of the tubers.

The behavior of a comparatively large number of varieties under widely different conditions indicates that resistance to scab occurs in the potato in varying degrees. Complete immunity has not as yet been demonstrated. Concerning this point, Berkner (*3*) says that absolute immunity does not appear to exist, but that there are decided

hereditary differences in the degrees of resistance and susceptibility.

The nature of resistance to scab has been studied by several investigators. The fact that the varieties that have shown the highest degrees of resistance possess a thick russet skin has led some to believe that resistance is dependent upon this type of skin. Histological studies of several varieties by Lutman (*37*) led him to conclude that thickness of skin determines the resistance of the tubers to scab and that color does not play an important role. Stuart (*70*) showed the fallacy of the prevailing conception that the russet type of skin is the basis of freedom from scab and pointed out that scab was abundant

Figure 5.—Two seedlings of a progeny segregating for resistance to late blight: No. 319 (left) practically free from late blight; no. 320 (center) completely killed by this disease. At right, susceptible Green Mountain check. August 21.

on the tubers of Cambridge Russet during a period of 6 years. In tests of a large number of seedlings, Darling, Leach, and Krantz (*21*) found a high degree of resistance in smooth and thin-skinned seedlings as well as in russet types. No correlation was shown to exist between color of tuber and scab resistance.

Some of the American commercial varieties, such as Russet Rural, Russet Burbank, and Mahr Russet, have been known for a number of years to be resistant to scab. A number of European varieties, Richter Jubel, Arnica, Hindenburg, Oststarke, Treff As, Rheingold, and Ostragis, are also resistant, as was reported by Schlumberger (*62*, *63*). These varieties, with the addition of a U. S. D. A. seedling, no. 44537, which is highly resistant to scab, have become the basis of breeding for resistance to this disease. At Presque Isle, Maine, a large

number of other varieties also have been tested for the purpose of obtaining additional material. The first tests, 1930–33, were conducted on land that was known to produce scabby potatoes in previous years. The results were somewhat variable. In 1934–36 lime was applied, before planting, at the rate of about 1 ton per acre, to land that was known to produce some scabby potatoes in previous seasons.

In the tests five hills of the variety or seedling to be tested were planted in alternate hills with Green Mountain, which is susceptible to scab. Comparisons were made between the seedling or variety and the Green Mountain check. The material included in these tests

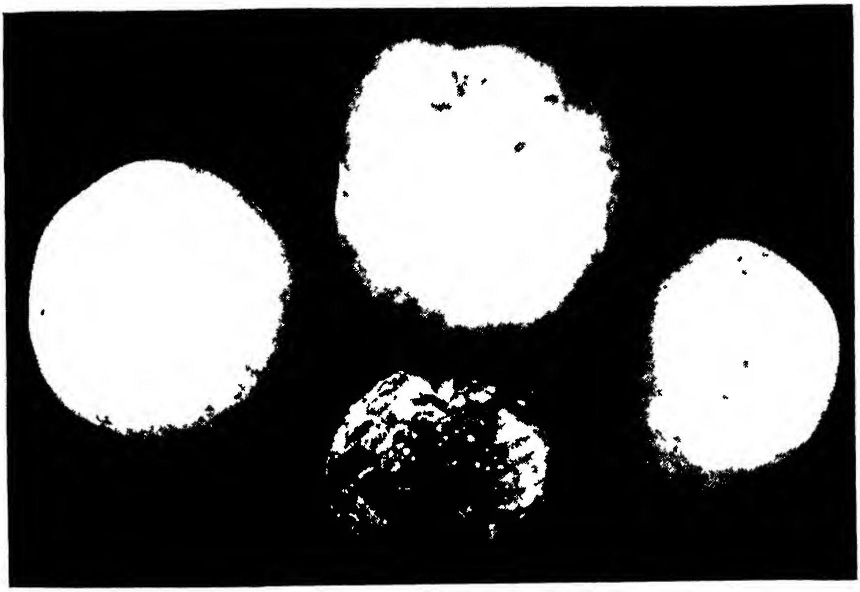

Figure 6.—Resistance of tubers to late blight. Sound tubers, seedling no. 336–302; decayed tuber, Green Mountain. Both lots artificially inoculated with spores of the organism that causes late blight.

consisted of varieties of North American, European, and Asiatic origin, a collection of South American varieties obtained by the MacMillan-Erlanson expedition, and a number of progenies resulting from selfing certain varieties, as well as progenies from crosses. Several of the European varieties, including Hindenburg, Richter Jubel, Ackersegen, Arnica, and Hindenburg × Centifolia No. 9, which had been introduced because of their resistance to this disease, proved to be highly resistant in the scab test plots. All of these produced less than 1 percent of the amount of scab found on the Green Mountain checks. None of them had enough scab lesions on the tubers to classify them as scabby potatoes, while the Green Mountain tubers could not have been sold for table stock.

Golden, a new variety recently produced by the Department, was found in the 1935 tests to have about one-fifth as much scab on the

tubers as was found on the Green Mountain checks. A few North American varieties—Russet Rural, Russet Burbank, and Mahr Russet—were intermediate in their resistance. A relatively large number of crosses have been made in an effort to determine the breeding behavior of some of these varieties. Although the data will not permit the formulation of an exact genetic hypothesis, a number of facts have been brought out in these tests. The progeny of a cross between two scab-susceptible varieties, Columbia Russet and Katahdin, were all susceptible. Another cross between two resistant varieties, Ostragis and Hindenburg, produced a progeny in which all were resistant to scab. Other crosses between resistant varieties showed segregation for resistance in the first generation

Figure 7.—**Resistance to common scab. The second and third tubers, seedling no. 416–50, are highly resistant to this disease. The first and fourth tubers are from the Green Mountain check grown in the hills adjacent to the seedling variety.**

A heavily russeted seedling variety, no. 44537, proved to be highly resistant to scab. This variety produces good pollen and is self-fertile. A progeny of the variety, selfed, segregated for resistance and russeting. A number of the russeted types and a few of the smooth white-skinned segregates were resistant to scab. This variety has been crossed with susceptible and resistant varieties. The progenies of certain combinations segregated for resistance and susceptibility. Figure 7 shows a resistant segregate in comparison with the Green Mountain check. One of the most promising progenies from the standpoint of both resistance and vigor resulted from a cross between Richter Jubel and seedling no. 44537. This progeny segregated for russet and smooth skin and for resistance and susceptibility to scab. A large number of both the russet and the smooth types were resistant to scab. A number of these were desirable from the standpoint of shape, depth of eye, color of tuber, and vigor, as well as scab resistance, and were selected for future work. It is too soon to predict their commercial possibilities, but some of them are the most promising scab-resistant seedling varieties produced so far.

Practical Results

The foregoing results show progress. A practical accomplishment has been the distribution within the last 5 years of six new varieties of potatoes. Others are on the way. Warba and Red Warba have been distributed by the University of Minnesota, and four varieties—Katahdin, Chippewa, Golden, and Houma—by the Department. Warba is an early variety, and from reports from different sections of the country it seems to be outstanding among the early varieties in yielding ability. Red Warba has not been tested thoroughly, but it is assumed to be similar to Warba in all its characters except color, since it originated from that variety as a vegetative mutation.

The four new varieties distributed by the Department in cooperation with the State experiment stations are all resistant to the virus disease mild mosaic, which causes so much running out of the Green Mountain variety in Maine. Chippewa is being increased as rapidly as the available supply of seed stock will permit. It is medium early, has high yielding ability, and is widely adapted. Golden is a yellow-fleshed variety, like most of the potato varieties used for food in Germany. There is a limited demand for this type in the United States, and Golden is being grown by 50 or 60 growers in Maine and by a few in the Upper Peninsula of Michigan. The variety is not widely adapted, but where it can be grown successfully it is prized because of its very high yields, good cooking quality, and scab resistance.

Houma was selected from a group of U. S. D. A. seedlings grown at Houma, La., by J. C. Miller, of the University of Louisiana, because of its high quality and adaptation to the Houma potato-growing section of that State. The season just past showed this variety to be somewhat drought resistant, but not sufficiently so to withstand the severe drought in the Middle West.

Katahdin (fig. 8) was the first variety to be introduced by the Department, and for that reason it is the most widely known of the Department introductions. It has had its ups and downs but is still on the increase. In a recent bulletin Moore and Wheeler (*40*) say in part:

> An outstanding characteristic of the Katahdin that should appeal to most Michigan growers is its ability to produce satisfactory yields of good type tubers even under heat and drought conditions. The Katahdin sets fewer tubers per hill than the Rurals and develops them earlier. This characteristic often enables it to surpass Rurals in yield of marketable potatoes, particularly when the season is unfavorable for the Rural varieties. The results of tests and the experiences of many growers confirm this statement.

Four seasons unfavorable for Rurals but in which Katahdins have been grown successfully have occurred in Michigan since 1930. This is no doubt responsible for the fact that most of the 500,000 bushels of Katahdins grown in Michigan in 1935 were kept for the 1936 planting, although it is not definitely known how the market will receive this variety. Preliminary tests have shown that the Katahdin as grown in Michigan is superior to the standard varieties in market quality and is equal at least to the Rurals in cooking quality. In the fall of 1935, 53 bushels of Katahdin were distributed in bushel lots to 53 hotels in Michigan, Ohio, Illinois, and Indiana.

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Fourteen hotels had a few criticisms to make. Thirty-nine reported that they found the Katahdin an excellent potato for baking, boiling, and frying, and that they were well pleased with the color and texture of the cooked product. Many of the hotel chefs made favorable comments on the attractive appearance of the Katahdin and were

Figure 8.—A field of Katahdin. Note vigorous vine growth almost covering rows.

well pleased with its smooth, thin skin and shallow eyes, which reduced waste in peeling.

These same characteristics, smooth shape and shallow eyes (fig. 9), combined with the resistance to mild mosaic, induced the representative of Argentina, looking for seed potatoes in the United States and Canada, to recommend the purchase of a large quantity of seed stock of the Katahdin variety for that country. He is said to have purchased a quantity of Chippewa, too, although the price of these was comparatively very high. He refused to consider the deeper eyed types such as Irish Cobbler and Triumph.

The potato-breeding project as it now stands and the results up to the present time demonstrate clearly the necessity and the advantages of cooperation in scientific enterprises. The project is dependent on the Division of Plant Exploration and Introduction, Bureau of Plant Industry, United States Department of Agriculture, for new material carrying new genes for resistance and other important characters. Within recent years varieties resistant to late blight, others resistant to scab, and still others that are said to be resistant to leaf roll have been obtained. The plant breeders and horticulturists make the crosses and grow the progenies. The plant pathologists create the epidemics and secure the disease data. The Bureau of Home Economics of the Department, assisted by the horticulturists, makes the cooking tests. The State experiment stations cooperate in testing the new seedlings produced either by the Department or by

any other institutions to determine their range of adaptability. If any of the investigators find a seedling adapted to growing conditions in their State they take the responsibility of increasing the seed and seeing that it is distributed to growers. All these steps are necessary for the success of the breeding work, and all the organizations share the credit for its accomplishments.

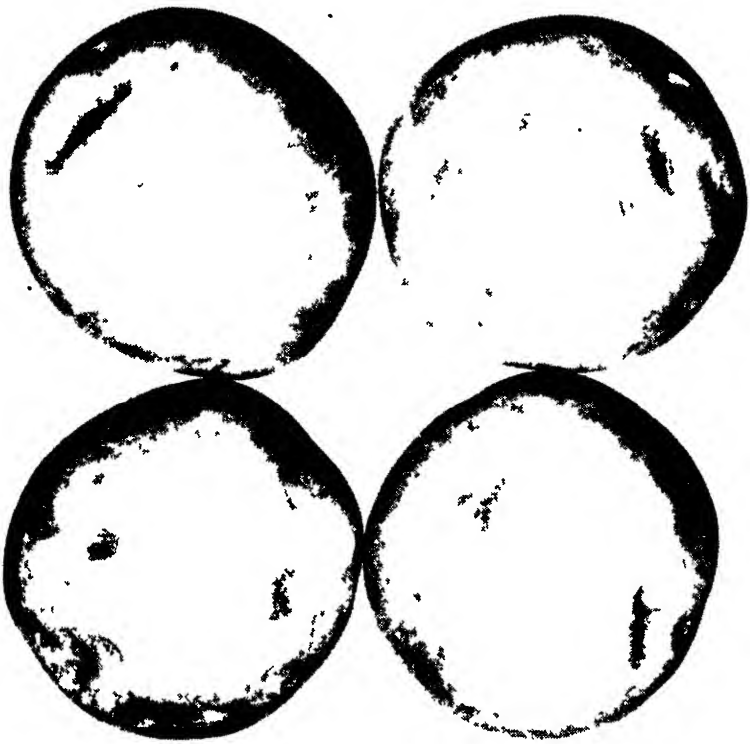

Figure 9.—Tubers of the Katahdin potato. The good shape of the tubers and the shallow eyes are outstanding features of this variety.

A summary of the results of breeding work up to the present time shows:

(1) A large number of varieties resistant to one virus disease, mild mosaic.

(2) One variety and several of its progenies immune to another virus disease, latent mosaic.

(3) Many varieties resistant to late blight, several showing commercial possibilities.

(4) A large number of varieties resistant to scab, too new to predict the possibilities.

(5) One variety as early as Irish Cobbler, but much smoother and with shallower eyes, being tested by farmers and about ready for naming.

(6) Six varieties named and distributed.

(7) The Katahdin and Chippewa firmly established as commercial varieties and entering into the South American seed trade because of their attractive appearance and disease resistance.

BREEDING METHODS, GENETICS, AND CYTOLOGY [2]

THE introduction of new varieties or species may not appear to be a plant-breeding procedure, yet it is fundamental to a well-rounded breeding program. It is improbable that varieties will be found in foreign countries adapted to any of the potato-growing regions of the United States, but even if the new introductions cannot compete with the standard varieties they may carry genes for certain characters that will make them extremely valuable from the breeding standpoint. For example, a number of varieties have been introduced recently from Europe that are resistant to late blight, others that are resistant to common scab, and still others that are reported to be resistant to leaf roll. These are being used in crosses for the purpose of combining the genes for resistance with those for other characters of economic importance. In the last 30 years approximately 10,000 sorts, including commercial varieties, seedling varieties, and species, have been collected by the Department. Thousands of these have been discarded because they were considered of no value, but others have provided a wealth of material for the work of potato breeders.

ADVANTAGES AND LIMITATIONS OF THE METHODS USED

Selection is the principal tool of the plant breeder regardless of the method employed. Selection of clons or strains from a variety has often been designated as a special method. This method is limited in its application, since its success depends on the value of the bud sports or mutations that occur in a variety or clonal line.

Varietal crossing has been universally employed by potato breeders. As a rule, varieties are heterozygous or mixed in their inheritance for most characters and they will segregate into different lines when they are self-pollinated. Because of pollen sterility not all varieties can be selfed, and the only way to use valuable genes in a self-sterile variety is to make it a female parent in crosses. If both parents are heterozygous for the characters under consideration, segregation will take place in the first generation. Not all possible recombinations of characters can be expected in the first generation, however, since one of the parents may be homozygous or pure for some dominant character, in which case all the plants of the first generation would resemble that parent in that particular character. As an example, in some instances the first generation of a late variety crossed with an early may be all late, no segregation into late and early lines appearing. There are certain advantages in using crosses between heterozygous material, and also certain disadvantages. One advantage is that segregation occurs in the first generation; and if, because of sterility, a second generation cannot be produced, it may be possible in many instances to obtain the desired recombination in the first generation. Another advantage is that combinations differing widely in vigor often occur when heterozygous parents are used, and individuals are often found more vigorous than either parent. The main disadvantage in the use of heterozygous lines as parents is the difficulty of obtaining exact genetic knowledge of the breeding material.

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[2] This section is written primarily for students or others professionally interested in breeding or genetics.

Sib mating, or sister-brother mating, is one system of inbreeding and is useful for several purposes. It helps to determine the degree of homozygosity or uniformity of inheritance of a particular line. Selfing each of the sibs would of course give the same information, but this cannot always be accomplished because of the self-sterility of many lines. In some cases, too, segregates from a cross between two sibs are more vigorous than either parent.

Backcrossing is employed to good advantage in potato breeding, but as most of the parent material is heterozygous, it is not so efficient as if homozygous lines were available. If the original parents are homozygous all the plants of the first generations have the same inheritance although they differ in appearance, and a backcross to any one of them gives essentially the same results as it would to any other. If parents heterozygous for certain characters are used, the first-generation hybrids may differ genetically among themselves, and therefore would give different results in backcrosses. More work must be done to accomplish the same results when heterozygous parents are used than would be necessary if vigorous fertile homozygous parents were available. But in any case backcrossing is a useful method, and it is employed very frequently to obtain certain combinations of characters.

Selfing is employed at least to some extent by all plant breeders. Selfing and the recombining of selfed lines is being used extensively by corn breeders, but potato breeders have depended to a large extent on other methods to obtain desirable recombinations. The self-sterility of many clonal lines and the loss of vigor brought about by intensive selfing are probably two of the reasons why potato breeders have not generally adopted this method. Another reason is that the potato as grown commercially is propagated from tubers, and the grower gets a comparatively uniform crop even if the variety is heterozygous for certain characters. This is not true with crops propagated from seed, as these must be genetically uniform in order that a uniform crop may be produced. For genetic studies it likewise is desirable to obtain homozygous potato lines that are fertile. From the commercial standpoint some of the most promising material is obtained by selfing one or two generations, selecting the best of these selfed lines and outcrossing to one of the best commercial varieties. This method has sometimes been referred to as top crossing.

Strain building is not a method in itself but is a system of breeding that makes use of all methods. The system can best be described by an example from the disease-resistance work now in progress at Presque Isle, Maine. A few blight-resistant varieties were obtained from foreign countries, and several seedling varieties produced by the Department were selected that were only slightly injured by the blight epidemic of 1932 in the breeding plots at Presque Isle. The most promising of these from the standpoint of blight resistance were crossed with varieties carrying genes for high yield, good shape, shallow eyes, resistance to mild mosaic, and other characters of economic importance. The progenies were tested for blight resistance, and the most promising seedlings were selected. Some of these were selfed, some of them sib-mated, some backcrossed to the resistant parent, and others outcrossed to unrelated blight-resistant varieties. The

resulting progenies were again tested for blight reaction and selections made, taking into consideration resistance to blight, shape and color of tuber, depth of eye, and vigor. By such a combination of the methods of introduction, varietal crossing, sib mating, backcrossing, and selfing, it should be possible to get any desired recombination of the genes of the parent cultures. Some of the resulting new varieties thus produced should be as good as or better than the commercial varieties in yield, shape of tuber, etc., and superior to them in disease resistance.

The use of species hybrids is usually the last resort of the breeder interested in the production of superior horticultural varieties. It is true that in order to do the best work he must be acquainted with the wild relatives of the plant with which he is working, the characters they possess, and their behavior in crosses. Research with species and species hybrids, then, must be one aspect of any breeding project. It sometimes happens that a desirable character is not to be found in the cultivated varieties of a crop but is present in a related species, so that the desired combination of genes can only be obtained by making a cross between species. An illustration of this is found in breeding potatoes for resistance to late blight. At present, although a number of cultivated varieties are resistant to this disease, none has been found immune to its attacks. Some of the related species, however, do show immunity. Attempts have been made from time to time to combine this immunity with characters of commercial importance by the use of species hybrids.

By the use of all the available methods, if it were not for sterility, the number of new varieties that could be produced through recombinations would be limited only by the characters of the available parents and the number of offspring it is possible to grow.

Sterility a Major Handicap

Sterility, or lack of fruitfulness, which is very generally present in potato varieties, is the source of the greatest difficulty in sexual breeding, and in spite of much study of the condition it remains the greatest handicap of the potato breeder.

Salaman (*51*, *52*) and Heribert-Nilsson (*24*) found sterility of the anthers to be dominant to fertility. At first Salaman believed sterility was due to a single gene, but later Salaman and Lesley (*59*) indicated a more complex manner of inheritance. Edzell Blue, a variety that produces viable pollen, was heterozygous on its female side for male sterility. Krantz (*32*) points out that two commercial varieties, Green Mountain and Early Ohio, have produced fertile seedlings in progeny grown from self-fertilized seed. The Green Mountain variety usually sets some seed under favorable growing conditions. The Early Ohio variety sets no seed. It apparently produces viable pollen under very favorable circumstances.

Kessler (*27*) described a number of morphological characters of the pollen of various varieties and their relation to its germinating power. Neither the shape in itself nor the amount of granulation was an indication of sterility. A much surer test was obtained by staining with carmine in hydrochloric acid. The sterile pollen remained unstained. The influence of culture media, air, humidity, temperature, and light was considered. Light had an adverse effect, as had also temperatures

above 95° and below 46° F. Studies of pollen tube development after artificial pollination indicate that the pollen tube of a particular variety may reach the ovule successfully when applied to certain varieties but not when applied to others.

Clark (*14*) enumerates four different types of plant sterility—premature abscission or dropping of buds and flowers, lack of viable pollen, hybridity, and physiological incompatability between parents.

Premature abscission constitutes a very effective type of sterility, since it is obvious that fruit cannot be produced when buds fall before opening or flowers persist for only a few hours. If this is not very pronounced, so that a few flowers open and persist for a few days, they may, under favorable climatic conditions, produce fruit when pollinated with viable pollen. The anthers of such flowers produce little pollen, and this is rarely, if ever, viable.

Pollen sterility is very strongly manifested in the cultivated varieties of potatoes. This condition appears to be inherent in the species. Stout and Clark (*68*) studied the pollen of 170 commercial varieties and 513 seedling varieties, representing material from many parts of the world. They failed to find a single variety in which there was not a fairly large percentage of sterile pollen. Of seven wild species studied, only one, *Solanum commersonii* Dun., showed the presence of this type of sterility to any marked degree.

Salaman (*51*) demonstrated the hereditary nature of sterility in potato a number of years ago. He stated that the potato plant, which is normally bisexual, carries a dominant factor that inhibits pollen formation at the pollen mother cell stage or even earlier. In a later paper Salaman and Lesley (*59*) showed by reciprocal crosses that the greater portion, if not all, of the sterility is inherited through the female parent. The fact that the eggs are often viable under conditions lethal to the pollen is well known and makes possible the use of many varieties as seed parents that cannot be used as pollen parents.

Irregular chromosome behavior has been advanced by a number of investigators as one of the chief causes for hereditary sterility. Longley and Clark (*36*) presented a study of chromosome number and of meiotic behavior in tuber-bearing forms of *Solanum*. In 37 cultivated varieties grown in the United States there was found a somatic chromosome number of 48. The meiotic behavior of this group varied from regular in a few cases to extremely irregular in many of the varieties. Only the few varieties with a regular chromosome behavior produced an appreciable amount of viable pollen; varieties with an irregular chromosome behavior produced practically no pollen.

Genetic factors and chromosome behavior no doubt make the development of sterility possible, since varieties are inherently different in the degree to which they will bloom or set seed. But seed setting is also influenced by environmental factors to a marked degree. Some varieties will set seed under a wide range of conditions, while others have never been known to set seed even under favorable conditions. Stow (*69*) showed that environmental conditions even influenced the chromosome behavior. He stated that—

> the abnormal division is neither connected with the hybrid nature of the plant nor the nutritive correlation within its body; but is rather due to the environmental conditions or certain special nature of the plant itself.

He considered that sterility was mainly the result of abnormal pollen mother cells, which he observed with exposure to high temperatures (25°–35° C.). "At lower temperatures (15°–20° C.), on the other hand, the reduction proceeded in a regular manner, producing normal pollen grains."

That length of day has an influence on flowering and seed setting has been shown by Stevenson and Clark (*66*). In the experiment reported by them that was conducted in the greenhouse at the Arlington Experiment Farm, Arlington, Va., the application of artificial light for 5 hours to 20 potato varieties to supplement the daylight period stimulated vine growth and blossoming to a remarkable degree. The varieties used in this experiment were grown also in the field at Presque Isle, Maine, where 10 of them produced seed in varying degrees of abundance, while the remaining 10 produced no seed. In the greenhouse experiment at Arlington, 70 percent of the plants in the 10 more responsive varieties came to full bloom under the lights, while only 5 percent of the checks without lights bloomed. In the less responsive varieties only 20 percent of the plants under the lights bloomed, and no blossoms were produced by the check. No naturally fertilized seed was produced, but inbred seed was readily obtained under the lights by hand-pollinating self-fertile plants. The chromosome behavior of the plants grown under the light was much more regular than that of the same varieties grown without lights.

The effect of environment on blooming was shown by Stout and Clark (*68*). Halved tubers of 15 varieties were grown, one set at Presque Isle, and the corresponding halves at the New York Botanical Garden. All the varieties bloomed profusely at Presque Isle. In New York only 2 of these varieties bloomed well, 3 produced a few flowers, and 10 produced no flowers that opened. Conditions are favorable for seed setting nearly every season at Presque Isle. A few other places in the United States have been found favorable for seed production in potatoes. At Estes Park, Colo., which has an elevation of 7,500 feet, seed sets in most years quite readily. Another striking example of the effect of environment is found in the potato-breeding work in Minnesota. Seed cannot be produced on a large number of varieties and strains at University Farm, St. Paul, but many of the same varieties will produce seed at Duluth on Lake Superior, and even better at Castle Danger on the north shore of the lake.

Complete or partial sterility may result from hybridizing, though there seems to be no general rule regarding the behavior of hybrids with respect to sterility, as some combinations produce hybrids with a very high degree of fertility, while the progeny resulting from other crosses may be completely sterile. In a species cross between *Solanum fendleri* A. Gray and *S. chacoense* Bitt., produced by Clark (*15*), the first generation was completely sterile when selfed and when backcrossed with either parent. Bukasov (*10*) reports that hybrids of *S. acaule* Bitt. with *S. andigenum* and with *S. tuberosum* are sterile.

In some species of plants certain combinations of crosses within the species as well as selfed pollinations fail to produce seed even though there is no degeneracy in either pollen or egg cells. Other combinations in the same species may produce an abundance of fruit. This type of sterility has been referred to as physiological incompatibility.

It was not found to occur in the cultivated varieties of potatoes studied by Stout and Clark (*68*), but was reported by Clark (*14*) to be present in the wild species *Solanum caldasii glabrescens* Dun. and *S. chacoense*.

Genetics of the Potato

Definite genetic data are available for only a comparatively few characters of the potato. Such data are accumulating from year to year, however, and as the knowledge grows the solution of many breeding problems becomes less complex. A partial summary of potato characters, their genetic behavior, the name of the investigator making the report, and the literature citations are given in the appendix.

A study of the table shows the usual array of gene interactions—dominance and recessiveness, complementary genes (either 2 or 3), multiple genes, cumulative effects, and inhibiting genes.

In several instances a number of different ratios are reported for what is apparently the same character; but it must be remembered that characters that look alike may be genetically different and as a result will behave differently in inheritance.

From the material available it is seen that little is known concerning the genetic behavior of some of the most important characters of the potato, such as yield, cooking quality, and resistance to various diseases, but the breeding work is being centered around such characters at present, and it is believed that, while they may be rather complex in their genetic behavior, they will all follow the general rule that a genetic character is the end result of the interaction of genes and environment.

Potato Species, Their Chromosome Numbers, and Some of Their Valuable Characters

While it is necessary for the breeder to obtain a thorough knowledge of the cultivated varieties and their important economic characters, it is also important to know the related wild forms and species of potatoes. It is true that new genes and gene combinations are being brought to light in the cultivated varieties, but it is quite improbable that all the problems can be solved by the recombinations of genes available in this group.

Much work has already been done with the species of *Solanum* related to the potato, and a fund of valuable information is available concerning them. The species fall into five groups with respect to $2n$ chromosome numbers, those having 24, 36, 48, 60, and 72 in vegetative tissues, as reported by several investigators. According to Bukasov (*9*), cultivated varieties have been found in the first four groups. Crosses between species with different chromosome numbers are as a rule difficult to obtain. For example, crosses between species of the 24 group and the 48 group are very rare, although many attempts have been made to produce them. Certain species crosses have been reported, however, and as knowledge increases concerning the causes of incompatibility and sterility, it may be possible in the future to get hybrid combinations that at present seem quite impossible. A partial list of species of the *Tuberarium* section of *Solanum*, with their $2n$ chromosome numbers, is given in the appendix.

Characters that would be especially valuable if they could be combined with those of the best commercial varieties have been found in a number of species. Among these are resistance to drought, frost, potato wart, viruses, and late blight. The characters for short-day development and short rest period are found in some of the species also. The character for short-day development might be valuable in potato districts where the crop is grown during the winter months under conditions of short-day length. A list of the species known to possess valuable characters from the breeding standpoint is also given in the appendix.

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APPENDIX

Early breeders of potatoes and the varieties originated by them

Breeders	*Varieties*
O H Alexander, Charlotte, Vt	Charles Downing, Dakota Red, Everett, Garfield, Green Mountain, Reliance, Trophy, White Mountain
Martin Bovee, Northville, Mich	Bovee, Early Michigan, Pingree
Albert Bresee, Hubbardton, Vt	Early Rose, King of the Earlies, Peerless, Prolific
C W Brownell, Essex, Vt	Beauty, Best, Centennial, Early Telephone, Eureka, Superior, Winner, Vermont Beauty
Luther Burbank, Lancaster, Mass	Burbank (Burbank's seedling)
E S Carman	Carman No 1, Carman No 3, Rural New Yorker No 2, Sir Walter Raleigh
E L Coy, Hebron, N Y	Early Beauty of Hebron, Late Beauty of Hebron, Early Puritan, Empire State, Late Rose, Noroton Beauty, Thorburn, Vaughan, White Elephant
Thomas Craine, Fort Atkinson, Wis	June Eating, Keeper, Potentate
C E Goodrich, Utica, N Y	Calico, Cuzco, Early Goodrich, Garnet Chili, and several others which were short lived in the commercial trade
D W Heffron, Utica, N Y	Chicago Market, Climax
C G Pringle, Charlotte, Vt	Alpha, Adirondack, Rubicund, Ruby, Snowflake
Arthur Rand, Shelburne, Vt	Champion, Delaware, Matchless, Improved Peachblow, Silver Skin
Alfred Reese	Early Ohio
G T Safford, North Bennington, Vt	Gold Coin
F B Van Ornam, Lewis, Iowa	Extra Early (Burpee's), Great Divide

TABLE 1 —*Potato varieties available in the United States known to have characters of value to breeders*

Variety	Source	Superior characters
Katahdin	Department of Agriculture	Fertility, resistance to mild mosaic good shape high yield
Chippewa	do	Resistance to mild mosaic, good shape, high yield, early tuber development
Golden	do	High yield, some resistance to scab
Houma	do	High yield, some drought resistance good shape good cooking quality
24642	do	Fertility, resistance to mild mosaic some earliness
41956	do	Immunity to latent mosaic and resistance to mild mosaic
44488	do	Resistance to late blight high yield
44537	do	Fertility, resistance to scab
45075	do	Fertility earliness good shape
45208	do	High yield, good cooking quality
45349	do	Resistance to late blight
46110	do	High yield
46125	do	High yield and cooking quality
46422	do	Fertility, yield
46923	do	Fertility and earliness
182 7	do	Fertility and resistance to late blight
336-7	do	Do
336-18	do	Do
336-123	do	High yield and resistance to late blight
336-144	do	Fertility and resistance to late blight
336-302	do	Resistance to late blight
3868-8	Department of Agriculture from German seed	Do
3897-90	do	Do

Table 1.—*Potato varieties available in the United States known to have characters of value to breeders*—Continued

Variety	Source	Superior characters
444-12	Department of Agriculture.	Fertility and resistance to scab.
Green Mountain	United States	High yield, quality.
Rural New Yorker No. 2	do	Good tuber type, hardiness.
Russet Rural	do	Do.
Russet Burbank	do	Good quality, resistance to scab.
Charles Downing	do	Good quality and tuber type.
Irish Cobbler	do	Earliness and wide adaptability.
Triumph	do	Earliness.
Early Rose	do	Do.
Early Ohio	do	Do.
Mahr Russet	do	Resistance to scab.
Warba	Minnesota	Earliness, yield.
Red Warba	do	Do.
Arnica	Germany	Resistance to scab.
Hindenburg	do	Do.
Richter Jubel	do	Fertility, resistance to scab.
Ostragis	do	Resistance to scab.
Rheingold	do	Do.
Ackersegen	do	Resistance to late blight.
Ekishirazu	Japan	Do.
No Blight	Canada	Do.
Paisley's No. 1	do	Do.
Paisley's No. 2	do	Do.
Paisley's No. 3	do	Do.
Paisley's No. 4	do	Do.
Imperia	do	Resistance to leaf roll.
Triumf	Netherlands	Do.
Albion	do	Do.
Friso	do	Do
West Brabander	do	Do.
Bevelander	do	Do.
Noordeling	do	Do.
130.5-24	North Carolina	High yield.
101-91	Michigan	Good tuber shape, high yield on muck.
155-29	do	Do.
155-49	do	Do.
401-23	do	Do.
472-10	do	Do.
472-33	do	Do.
472-53	do	Do
N. D. No. 64	North Dakota	High yield, good shape.
N. D. No. 82	do	Earliness, good shape.
N. D. No. 86	do	Earliness, high yield, and good shape.
N. D. No. 87	do	Russet.
F. B. 32-1	Colorado (Fort Collins).	High yield, good shape.
L. 32-1	do	Russet.
E. 32-7	do	Earliness, high yield, good shape.
E. 32-8	do	High yield, good shape.
252	do	Fertility, shallowness of eye.
C. S. 48	Colorado (Greeley)	Fertility.
C. S. 50	do	Do.
C. S. 98	do	Do.
C. S. 106	do	Resistance to fusarium.
C. S. 125	do	Do.
C. S. 133	do	Do.
C. S. 155	do	Do.

Table 2.—*Potato lines and progenies known to have superior genetic characters, produced by the U. S. Department of Agriculture and by the New York (Cornell) and Minnesota Agricultural Experiment Stations*

UNITED STATES DEPARTMENT OF AGRICULTURE

Cross no.	Parentage	Superior characters
774	S 41956 × Katahdin	Resistance to latent and mild mosaics.
792	S 41956 × S 45075	Resistance to latent mosaic.
926	Katahdin × S 45075	Earliness, resistance to mild mosaic.
1028	Katahdin selfed	Resistance to mild mosaic.
295	Russet Rural × S 44537	Resistance to common scab.
528	Richter Jubel × S 44537	Do.
336	No Blight × Katahdin	Resistance to late blight and mild mosaic.
618	S 45349 × Ekishirazu	Resistance to late blight.
690	S 45349 × Katahdin	Do.

TABLE 2.—*Potato lines and progenies known to have superior genetic characters, produced by the U. S. Department of Agriculture and by the New York (Cornell) and Minnesota Agricultural Experiment Stations*—Continued

NEW YORK (CORNELL UNIVERSITY) STATION

Line	Superior characters
500 hybrid families	Immunity from late blight.

MINNESOTA STATION

Line no.	Parentage	Generations inbred (selfed)	Sublines: Inactive	Sublines: Active	Superior characters
		Number	*Number*	*Number*	
1	Peerless	4	13	2	Early maturity, high pollen fertility, resistance to scab.
3	Cobbler × Peerless	4	11	3	Early maturity, vine type.
4	Keeper × Silverskin (U. S. 14329).	9	182	7	Early maturity, good tuber shape, high pollen fertility, free blooming.
5	Peerless × Lookout Mountain.	7	90	43	Early maturity, high pollen fertility, short stolons, resistance to scab.
9	Warba × Katahdin	1	0	1	Vine type, tuber quality, resistance to virus.
11	Inbred 41-17 × Inbred 4-9-1.	7	150	34	Early maturity, good tuber shape, high pollen fertility, vine type, vigor and yield, tuber set, free blooming.
12	Snowflake	5	29	3	Good tuber shape, vigor and yield, tuber quality.
13	Burbank × Inbred 66-1	2	0	2	Good tuber shape, tuber quality.
15	Inbred 11-1-25 × Inbred 66-5.	2	0	5	Early maturity, good tuber shape, high pollen fertility, vigor and yield, free blooming.
21	Inbred 49-1 × Inbred 4-9-1.	3	16	3	Early maturity.
29	Inbred 41-1 × Inbred 4-25.	3	30	2	Do.
39	Irish Cobbler	5	40	4	Early maturity, good tuber shape, vine type, tuber quality, short stolons, resistance to virus.
40	U. S. Seedling 38946	3	23	3	Good tuber shape, high pollen fertility, vine type, free blooming, resistance to virus.
41	Early Ohio	5	130	9	Early maturity, vine type, vigor and yield, tuber set.
66	Katahdin	2	0	13	Good tuber shape, tuber set, resistance to virus.
82	Inbred 11-1-25 × Inbred 21-2-2.	3	0	17	Early maturity, good tuber shape, high pollen fertility, free blooming.

TABLE 3.—*Potato characters, their genetic behavior, and the investigators and reference numbers*

Character	Genes and interactions	Segregations	Investigators and reference numbers
Flower color:			
Purple × white	Purple dominant to white		East (*22*).
Lilac × white	Lilac dominant to white		Fruwirth (*23*).
Blue violet × white	Blue violet dominant to white.	3 blue violet : 1 white	Müller (*41*).
Light blue (selfed)	Heterozygous	Monogenic	Heribert-Nilsson (*24*).
Light blue × white		1 colored : 1 white	Do.
Violet blue (selfed)	Multiple factors	Violet-blue, red, reddish purple, dark and light blue and white.	Do.
Red × white	2 complementary genes $D+R$ for red.		Salaman (*53*).
Purple × white	3 complementary genes $D+R+P$ for purple.		Do.
White × white		In some strains colored and white.	(Salaman) Matsuura (*39*).
White (selfed)		do	Do.
Light lilac (selfed)	Complementary	9 colored : 7 white	Clark and Stevenson (*18*).

Table 3.—*Potato characters, their genetic behavior, and the investigators and reference numbers*—Continued

Character	Genes and interactions	Segregations	Investigators and reference numbers
Tuber color:			
White (selfed)	Homozygous	All white	Salaman (*52*, *53*).
Red (selfed)	2 complementary genes $R+D$ for red.	9 red : 7 white	Do.
Dark purple × white.	3 complementary genes $R+D+P$ for purple.	13 purple : 12 red : 4 white (F_1).	Do.
Dark purple (F_1) selfed.		73 purple : 24 red : 75 white (F_2).	Do.
Light red × yellow	Heterozygous	1 red : 1 yellow (F_1), various grades of red, many having blue or dark-blue striping, also plants with colored eyes.	Heribert-Nilsson (*24*).
Yellow × yellow		Yellow and 10 percent blue black, blue, red or pale red.	Do.
White (*S. edinense* selfed).	*G* and *H* complementary, *Y* inhibitor.	13 colored : 40 white	Muller (*41*).
White (*S. edinense*) × white (*S. tuberosum*).	do	21 colored : 40 white	Do.
Parti-colored	3 genes complementary; *B*, basic, *D*, diluting, $M+D$= parti-colored pattern.		Kelly (*26*).
Do	Multiple allelomorphic series for uniformly colored parti-colored and white.		Collins (*20*).
Red skin color	3 genes complementary, $D+R$=parti-colored, $D+R+A$=uniformly colored.		Krantz (*33*, *34*).
Red cortical color	3 genes complementary, similar interaction as for skin color.		Do.
Red color	Genes complementary, $A+D$=parti-colored, $A+D+R$=uniformly colored; linkage between *A* and *R*.		Asseyeva (*1*).
Do	Genes complementary, $R+S+D$=red skin color, $R+S$=red eye color.	27 colored : 37 white, 9 red-eyed : 7 white-eyed.	Sirks (*64*).
Color	Genes complementary, $D+R$=red, $D+R+P$= purple, and *H* an incompletely dominant inhibitor.		Black (*4*).
Red (selfed)	2 genes complementary	9 colored: 7 white	Huber (*25*).
Purple (selfed)	Single gene, color dominant.	1 dark purple: 2 light purple: 1 white.	Krantz (*31*).
Colored (selfed)	Complementary, $C+I$= colored.		Müller (*41*).
Colored × white	$C+I$+inhibitor Z=white	All white	Do.
Tuber flesh color:			
Flesh color	Multiple genes		Black (*4*).
Do	2 genes, 1 giving yellow in plant homozygous or heterozygous, other homozygous only.		Huber (*25*).
Stem color:			
Red *v.* green	Single gene, red dominant		East (*22*).
Medium red (selfed)		1 dark: 2 medium: 1 light	Salaman (*52*).
Pigment	3 genes complementary, a fourth gene an inhibitor.		Müller (*41*).
Colored internodes	3 genes for color	36 blue:9 red:19 white for young internodes; 12 blue: 3 red: 1 white for old internodes.	Sirks (*64*).
Seedling and sprout color:			
Seedling color	3 genes complementary	Seedling color associated with flower, stem, and flesh colors.	Müller (*41*).
Seedling color (blue, red, green).	2 or 3 genes complementary.		Sirks (*64*).
Sprouts, blue purple *v.* red purple.	Single gene blue-purple dominant, same as *P* for tuber color.		Asseyeva (*1*).

TABLE 3.—*Potato characters, their genetic behavior, and the investigators and reference numbers*—Continued

Character	Genes and interactions	Segregations	Investigators and reference numbers
Habit of growth:			
Upright *v.* prostrate	At least 3 genes (multiple)	3 upright: 1 prostrate. 15 upright: 1 prostrate. 63 upright: 1 prostrate.	Salaman and Lesley (*58*).
Tuber shape:			
Round (selfed)		All round [1]	Salaman (*52*).
Oval (medium long) (selfed).		Long: oval: round [1]	Do.
Long (selfed)		All long [1]	Do.
Medium round (selfed).		Range from round to long	Clark and Stevenson (*18*).
Round (selfed)		Not all round	Heribert-Nilsson (*24*).
Tuber shape	Dependent on more than 1 gene.		Black (*4*).
Do	Three genes (multiple)		Huber (*25*).
Do	At least 4 genes (multiple)		Bartosh (*2*).
Depth of eye:			
Deep (selfed)	Deep incompletely dominant to shallow.	All deep eyed	Salaman (*52, 53, 54*).
Medium deep (selfed).		Deep, medium, shallow	Do.
Shallow (selfed)		All shallow	Do.
Deep *v.* shallow	Shallow eye dominant		East (*22*).
Time of maturity:			
Late × late		Wide range of variability in F_2.	Krantz (*31*).
Time of maturity	Multiple genes		Krantz and Hutchins (*35*). Müller (*42*).
Inheritance of cropping:			
Heavy *v.* light	2 or more genes, heavy dominant.		Salaman (*56*).
Immunity and resistance to potato wart:			
Immune (selfed)	Homozygous	All immune	Salaman and Lesley (*60*).
Do	Single gene immune dominant.	3 immune: 1 susceptible	Do.
Do	2 genes duplicate	15 immune: 1 susceptible	Do.
Do	2 genes complementary	9 immune: 7 susceptible	Do.
Susceptible × slightly resistant.		F_1, 29 percent resistant	Heribert-Nilsson (*24*)
Susceptibility *v.* resistance.	Susceptibility dominant		Collins (*19*).
Do	Resistance dominant		Orton and Weiss (*45*).
Do	3 genes (multiple) with varying values and cumulative.		Black (*5*).
Resistance to late blight:			
Resistance *v.* susceptibility.	At least 2 genes acting independently.	Six types of segregation; no close linkage with commercial characters.	Müller (*43*).

[1] Similar results were obtained by East (*22*), Fruwirth (*23*), and Krantz (*31*).

Somatic chromosome numbers of potato species (2n)

Chromosome numbers and species	*Investigators and reference nos.*
24 chromosomes:	
Solanum ajanhuiri Juz. and Buk.	Kovalenko and Sidorov (*29*), Rybin (*49*) Vesselovskii (*72*).
S. aracc-papa Juz	Rybin (*49*).
S. boyacense Juz and Buk	Do.
S. brevidens Phil	Do.
S. bukasovii Juz	Rybin (*48, 49*).
S. caldasii Humb. and Bonl	De Vilmorin and Simonet (*73, 74*).
S. caldasii glabrescens Dun	Longley and Clark (*36*).
S. chacoense Bitt	Smith (*65*), Longley and Clark (*36*), Rybin (*48*), Oppenheimer (*44*).
S. cuencanum Juz. and Buk	Bukasov (*10*).
S. fernandezianum Phil	Rybin (*49*).

Somatic chromosome numbers of potato species (2n)—Continued

Chromosome numbers and species	*Investigators and reference nos.*
S. goniocalyx Juz. and Buk	Bukasov (*9*).
S. jamesii Torr	Smith (*65*), De Vilmorin and Simonet (*73, 74*), Longley and Clark (*36*).
S. kesselbrenneri Juz and Buk	Bukasov (*10*).
S. looserii Juz	Rybin (*49*).
S. phureja Juz. and Buk	Kovalenko and Sidorov (*29*), Rybin (*49*).
S. polyadenium Greenm	Longley and Clark (*36*).
S. rybinii Juz. and Buk	Rybin (*49*).
S. stenotomum Juz. and Buk	Rybin (*49*), Bukasov (*10*).
S. vavilovii	Bukasov (*10*).
36 chromosomes:	
S. cardiophyllum Lind	Rybin (*49*).
S. cardiophyllum f. *coyoacanum* Buk.	Longley and Clark (*36*).
S. chaucha Juz. and Buk	Kovalenko and Sidorov (*29*), Rybin (*49*).
S. chocclo Buk and Lechn	Bukasov (*9*).
S. commersonii Dun	Longley and Clark (*36*), Rybin (*49*).
S. coyoacanum Buk	Rybin (*49*).
S. juzepczukii Buk	Kovalenko and Sidorov (*29*), Pissarev (*46*), Rybin (*49*).
S. maglia Schlecht	Rybin (*49*).
S. mammilliferum Juz. and Buk	Do.
S. medians Bitt	Rybin (*48*).
S. riobambense Juz. and Buk	Bukasov (*10*).
S. tenuifilamentum Juz. and Buk.	Rybin (*49*).
S. vallis-mexici Juz	Kovalenko and Sidorov (*29*), Rybin (*49*).
48 chromosomes:	
S. acaule Bitt	Kovalenko and Sidorov (*29*), Rybin (*49*).
S. ajuscoense Buk	Do.
S. andigenum Juz. and Buk	Rybin (*49*).
S. antipoviczii Buk	Kovalenko and Sidorov (*29*), Rybin (*49*).
S. colombianum trianae Bitt	Rybin (*48*).
S. edinense Berth. (some forms).	(Campin), Salaman (*55*).
S. fendleri A. Gray	Smith (*65*), Longley and Clark (*36*), Rybin (*49*).
S. leptostigma Juz	Rybin (*49*).
S. tuberosum L	De Vilmorin and Simonet (*73*), Longley and Clark (*36*), Pissarev (*46*), Rybin (*49*).
60 chromosomes:	
S. curtilobum Juz. and Buk	Bukasov (*9*), Kovalenko and Sidorov (*29*), Rybin (*49*), Vesselovskii (*72*).
S. edinense Berth. (some forms).	(Campin) Salaman (*55*), Rybin (*48*).
S. semidemissum Juz	Kovalenko and Sidorov (*29*), Rybin (*49*).
72 chromosomes:	
S. demissum Lindl	Smith (*65*), De Vilmorin and Simonet (*74*), Longley and Clark (*36*), Pissarev (*46*).

Potato species known to have characters of breeding value, grouped according to these characters

Characters and species	*Investigators and reference nos.*
Frost resistance:	
Solanum acaule Bitt	Pissarev (*46*), Vesselovskii (*72*), Schick (*61*).
Solanum ajanhuiri Juz. and Buk.	Do.
Solanum andigenum Juz. and Buk.	Kovalenko (*28*), Bukasov (*9*), Vesselovskii (*72*).

***Potato species known to have characters of breeding value, grouped according to these characters*—Continued**

Characters and species	*Investigators and reference nos.*
Frost resistance—Continued.	
Solanum bukasovii Juz	Bukasov and Lechnovitz (*11*), Pissarev (*49*).
Solanum commersonii Dun	Bukasov and Lechnovitz (*11*).
Solanum curtilobum Juz. and Buk.	Bukasov (*8*), Pissarev (*46*), Rasumov (*47*), Schick (*61*), Vesselovskii (*72*).
Solanum demissum Lindl	Bukasov (*7*), Kovalenko (*28*), Pissarev (*46*), Rasumov (*47*), Schick (*61*), Vesselovskii (*72*).
Solanum edinense Berth	Bukasov (*7*).
Solanum juzepczukii Buk	Bukasov (*9*), Pissarev (*46*), Rasumov (*47*).
Solanum millanii Buk. and Lechn.	Bukasov and Lechnovitz (*11*).
Solanum semidemissum Juz	Bukasov (*7*), Kovalenko (*28*), Vesselovskii (*72*).
Drought resistance:	
Solanum medians Bitt	Bukasov (*10*).
Solanum vavilovii	Do.
Late blight resistance:	
Solanum ajuscoense Buk	Kovalev (*30*).
Solanum antipoviczii Buk	Bukasov (*10*), Kovalev (*30*).
Solanum bulbocastanum Dun	Bukasov (*10*).
Solanum demissum Lindl	Bukosav (*10*), Kovalev (*30*).
Solanum henryi Buk. and Lechn.	Bukasov and Lechnovitz (*11*).
Solanum millanii Buk. and Lechn.	Do.
Solanum polyadenium Greenm.	Bukasov (*10*).
Solanum vallis-mexici Juz	Kovalev (*30*).
Solanum vorrucosum Schlecht	Bukasov (*10*).
Virus resistance:	
Solanum rybinii Juz. and Buk.	Do.
Early maturity:	
Solanum phureja Juz. and Buk	Bukasov (*8*).
Solanum rybinii Juz. and Buk	Do.
Short-day adaptation:	
Solanum acaule Bitt	Bukasov (*9*).
Solanum antilobum	Pissarev (*46*).
Solanum antipoviczii Buk	Bukasov (*9*).
Solanum bulbocastanum Dun	Do.
Solanum demissum Lindl	Do.
Solanum goniocalyx Juz. and Buk.	Do.
Solanum juzepczukii Buk	Do.
Solanum semidemissum Juz	Do.
Solanum squamulosum Mart. and Gal.	Do.
Solanum vallis-mexici Juz	Do.
Solanum verrucosum Schlecht	Do.
Short rest period:	
Solanum boyacense Juz. and Buk.	Bukasov and Lechnovitz (*11*).
Solanum kesselbrenneri Juz. and Buk.	Do.
Solanum phureja Juz. and Buk	Do.
Solanum rybinii Juz. and Buk	Do.

STRAWBERRY IMPROVEMENT[1]

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THE strawberry came from North America, and some people think it is delicious enough to be a fair exchange for many of the fruits America has received from other parts of the world. Much of the work of developing the cultivated varieties has also been done in the United States; but so universal is the appeal of the strawberry that it is receiving the devoted attention of plant breeders in such remote lands as England, the Union of Soviet Socialist Republics (*47*)[2], and Japan (*33*, *34*, *35*, *36*).

The cultivated strawberry is definitely a product of plant breeding and is relatively young. The commercial development of this fruit has come principally since the Civil War, and most strawberry varieties now grown have originated within the past 45 years. Seventy years ago the strawberry was produced almost entirely near a few of the large cities. Now it is produced commercially in every State in the United States, as well as in the interior of Alaska. The introduction of improved varieties has been responsible for the steadily widening commercial production. When the first productive firm-fruited variety, Wilson, was introduced about 75 years ago, it became possible to grow the strawberry as far south as Florida and Louisiana. The hardy Dunlap, introduced about 35 years ago, made it reasonably safe to grow strawberries in northern Michigan, northern Maine, and parts of Canada. Later the origination of suitable high-quality varieties in Alaska made it possible to raise strawberries commercially even in that northern region. During the past century hundreds of thousands of seedlings have been tested, over 2,000 have been named, and a few score are widely grown; but these few score varieties combine the many qualities necessary for modern commercial production in every part of the United States and in every foreign country having a temperate climate.

The world-wide distribution of the strawberry may be attributed to three things: (1) The origination of firm varieties like the Wilson, adapted to widely different conditions; (2) the ability of the strawberry to grow from sea level up to elevations as high as 12,000 feet, in humid and dry regions, in the greenhouses of northern Europe,

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[2] Italic numbers in parentheses refer to Literature Cited, p. 482.

where the winter day is only 6 or 7 hours long, in Florida and southern California, where the winter day is 9 or 10 hours long, and in central Alaska, where the summer day may be 24 hours long (*17*); and (3) the high dessert quality and usefulness of the fruit, which matures in early summer when few fruits are available.

THE STRAWBERRY IS A TRAVELER

THE STRAWBERRY was born in North America, traveled to Europe, and finally returned home. But the strawberry that returned was very different from the one that went to Europe.

The cultivated strawberry of today is derived from two American species—the wild meadow strawberry (*Fragaria virginiana* Duch.) of eastern North America (figs. 1 and 2), and the beach strawberry (*F. chiloensis* (L.) Duch.), found along the Pacific coast from Alaska to California and along the coast of Chile (figs. 3 and 4). The beach strawberry is also found on the mountains of the Hawaiian Islands. The meadow strawberry has thin leaves and bright-red aromatic berries with deep-set seeds, and it grows freely in many soils and many

THE *work of the Department of Agriculture in strawberry breeding gives an excellent idea of the amount of detail involved in the production of improved varieties of plants. In Maryland, the Department has fruited 86,000 strawberry seedlings, representing artificial crosses among 150 different varieties. Of these, 1,999 were selected for further testing, and only 7 have been finally considered worth naming and introducing. In North Carolina, 54,000 seedlings have been grown and 1,245 selections have been made for further testing. In Oregon, the number of seedlings grown was 97,000 and the number selected for further testing is 1,331. In these few projects, then, more than a quarter of a million seedlings were involved; fewer than two out of a hundred were found to be worth further testing; and perhaps a score or fewer of new varieties will finally result. But of the few varieties already introduced, one is Blakemore, now considered to be the best preserving strawberry in the United States; another is Redheart, now more extensively grown than any other canning variety; and two others are Dorsett and Fairfax, which are superior in dessert quality to other varieties previously grown. In addition to this breeding work, 30,000 wild Rocky Mountain strawberries were collected in 1936 to be grown at Cheyenne, Wyo., with the idea of incorporating their superior resistance to cold, dry winters into cultivated varieties.*

locations. In contrast, the beach strawberry has thick leaves and dull-red berries with less aroma, and the seeds are usually raised above the surface. It is native only along the beaches. But hybrids are more vigorous and have wide adaptation.

First Improvement Was Made by American Natives

Before Columbus landed at San Salvador, unknown Indians of Chile, South America, had selected, from among the wild strawberries that grew only along the beaches, plants that bore fruit of exceptional size,

Figure 1.—The meadow strawberry of the eastern United States, *Fragaria virginiana.* The aroma, the beautiful color, and the wide adaptation of cultivated varieties come largely from this species.

"commonly as large as a walnut and sometimes the size of a hen's egg" (*48*). The fruit was pale red, with firm, meaty, almost white flesh and a delicate aroma (figs 3 and 4) More important, however, the selected plants, or at least one of them, had perfect flowers, while all the true wild beach strawberries and most of the wild meadow strawberries of North America have the sexes borne on separate plants (*61*). Just where the Indians found such a perfect-flowered wild plant, or how it came into cultivation, we do not know. An extensive search by the writer and others on the beaches of California, Oregon, and Washington has failed to locate a single perfect-flowered plant. One of the present needs in strawberry breeding is a survey of the coast of Chile, and particularly of Robinson Crusoe's island, Juan Fernandez, to locate plants having perfect flowers and to determine the value of the Chilean wild berries in breeding.

This early Chilean variety was taken to Peru in 1557, and it is still grown in Chile, Peru, Ecuador, and other South American countries.

The second important character in the story of the modern strawberry was a French officer, M. Frezier, who returned to Europe from Chile in 1714. He arrived at Marseilles, after a 6-month voyage, with five live plants of the Chilean variety (*48*). Plants of the meadow strawberry of eastern North America had already been taken to Europe, and from crosses of these two forms the modern strawberry was developed in Europe.

A third great character in the story was also a Frenchman, named Duchesne. In 1760, when only 19 years of age, he published a book of over 400 pages on the strawberry (*22*). He described the wild species, noted that some varieties had both pistils and stamens in their flowers and bore fruit, that others had only pistils and bore no fruit unless they grew near varieties that had stamens, and that still others had stamens and pistils but were sterile. Duchesne was probably the first to make actual crosses of strawberries.

Figure 2.—A pistillate-flowered seedling of a cross of the meadow strawberry (*Fragaria virginiana*) × Dunlap. Note the deep-set seeds.

A fourth character was an Englishman, Thomas Andrew Knight, who originated the Downton and later, about 1820, the Elton Pine, which is still grown in Europe (*29*). He made many crosses and proved that systematic breeding would result in improved varieties. He was really the world's first systematic fruit breeder. Best of all, he was a scientist who combined his scientific studies with practical breeding to secure better varieties. He has been followed by many strawberry breeders in England and on the Continent.

A fifth great character in strawberry history was Nicholas Longworth, a prominent horticulturist of Cincinnati, Ohio, and great-grandfather of Nicholas Longworth, the late Speaker of the United States House of Representatives (*11*, *12*). In spite of the work of Duchesne and a few others, few people in the United States knew there were different sex types in the strawberry. Longworth rediscovered these differences some time before 1834. He and his associates are said to have examined millions of strawberry flowers and classified plants into four groups—(1) pistillate, (2) hermaphrodite or perfect, (3) two rather rare classes having staminate flowers, and (4) a class having both pistillate and hermaphrodite flowers on the

Figure 3.—The Chilean strawberry (*Fragaria chiloensis*) as grown at Ambato, Ecuador, at an elevation of about 10,000 feet, where the rainfall is probably not over 15 inches a year. This is thought to be the same variety of strawberry that Frezier took to Europe in 1712 and that was grown by the Indians in Chile when Columbus discovered America.

same plant. Longworth found that not over one-third of the flowers of the hermaphrodite varieties ever set fruit, while all, or usually all, of the flowers of pistillate varieties set fruit. Longworth's work eliminated one great cause of failure in commercial berry production and made it possible to raise strawberries much more widely than before. Though the difference between pistillate and so-called perfect-flowered varieties has been common knowledge since the time of Longworth, much of his work on the degree of sterility of the

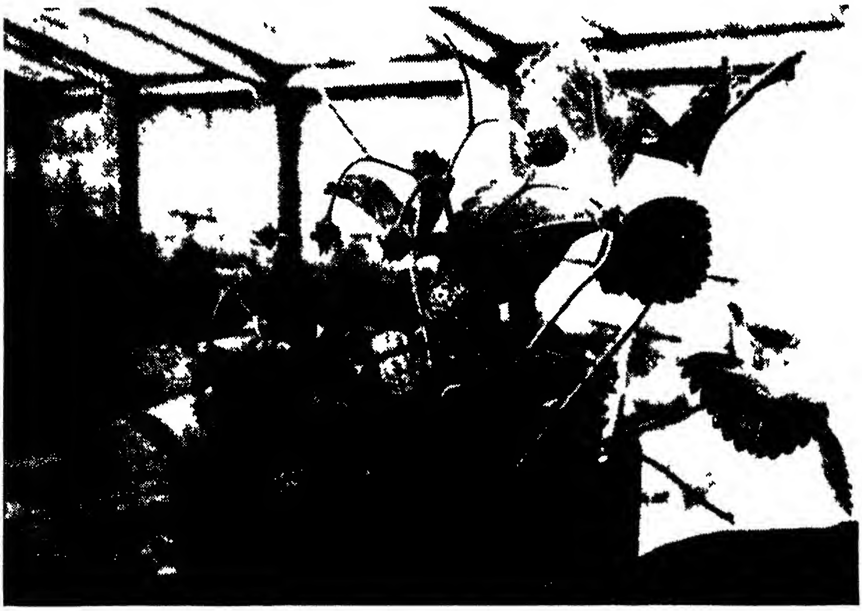

Figure 4.—The same variety of *Fragaria chiloensis* as in figure 3 but grown in a greenhouse near Washington, D. C., showing differences in shape and position of calyx (cap or hull). These berries were soft, while those shown in figure 3, grown in a cool, dry climate at a high elevation, are the firmest of any strawberries known in the world.

perfect-flowered varieties was lost sight of until rather recently, when it was rediscovered by Valleau (*60*) of Minnesota

Origin of American Varieties

The varieties originated in Europe were soon introduced into the United States, and many of them were grown extensively in this country, especially in the years before 1850. Commercial strawberry growing near the largest cities had begun in the United States about 1800, with such old varieties as Large Early Scarlet, Early Hudson, Hudson's Bay, Crimson Cone, Red Wood, and later the Hovey.

Since the time of Nicholas Longworth the outstanding development has been the introduction of a succession of new varieties with qualities that have made possible the extension of the territory where strawberries could be grown (*28*). Among the most important of these have been the Wilson, originated in 1851; Crescent in 1870; Sharpless

in 1872; Aroma in 1889; Dunlap and Marshall in 1890; Thompson in 1894; Klondike (*10*) about 1896; Missionary about 1900; Ettersburg 121 in 1907; Howard 17 in 1909; Progressive in 1908; Blakemore, Dorsett, and Fairfax in 1923; and Catskill in 1924 (*18*, *29*).

In England, Myatt introduced the British Queen in 1840, and Bradley originated the Sir Joseph Paxton in 1862 and introduced the Dr. Hogg in 1866. The Jucunda originated with Salter before 1860.

A large number of the other important English varieties were originated by Thomas Laxton and by his sons, the firm of Laxton Bros. With the encouragement of Darwin, Thomas Laxton began his strawberry breeding about 1865. His first variety was the Noble, introduced in 1884 and still grown extensively, especially in Germany and the Netherlands. In 1888 the King of the Earlies was introduced, and in 1892 the Royal Sovereign, a cross of Noble and King of the Earlies. Though British Queen and Dr. Hogg are the finest in quality in England, Royal Sovereign has high quality and is probably the most widely grown variety in northern Europe. Latest of All was introduced by Laxton Bros. in 1894, and Givons Prolific, raised by William Peters of Givons Gardens, was introduced in 1901. Bedford Champion was introduced by Laxton Bros. in 1904 and The Duke in 1919.

In France (*38*, *46*) Pelevain introduced Princess Royale in 1844, and it was said to have been the leading French variety for over 50 years. About 1856 the Vicomtesse H. de Thury, raised in 1845 by M. Jamin, was introduced; Marguerite was originated in 1859 by M. Lebreton; and in 1871 the Dr. Morere, raised by M. Berger, was introduced. Dr. Morere has been grown as widely in France as the Royal Sovereign in England.

In the Netherlands, Mme. Kooi was raised by G. Kooi before 1920 and introduced by R. Hendrikson, who also introduced the Mme. Lefèbre.

In Germany, Late Leopold, raised by L. Lierke, was introduced in 1904. Deutsch Evern, a cross of Sieger × Noble, was raised in 1902.

STRAWBERRY VARIETIES OF THE WORLD[3]

United States

A great many varieties have been grown in the United States, but at present only about 30 are important, 20 of them in about the order shown in table 1.

Besides the 20 listed, 11 other varieties make up about 4 percent of the total acreage (*18*). These varieties, with the same abbreviations for origin as in the table, are Catskill (Br), Clark (Br), Oelrich (Ulrich) (Ch), Ettersburg 121 (Br), Corvallis (Br), Glen Mary (Ch), Ridgely (Ch), Sample (Ch), Clermont (Br), Fairfax (Br), and Narcissa (Br). Though there are many other varieties in the trade, they are grown to a very limited extent.

Twenty-two of the thirty-one varieties were originated as the result of breeding, and they constitute over 75 percent of the acreage (*18*, *32*). For the most part, each of the important varieties has

[3] The strawberry species are described and listed in the appendix.

made its way rather quickly into a prominent position. Growers generally are interested in testing new sorts and are ready to change to any promising new variety. For example, the Howard 17 was introduced under that name in 1918, and 10 years later it was the principal variety north of the Ohio and Potomac Rivers. The Dorsett, introduced in 1933, has already become well known on the larger markets of the Eastern States.

TABLE 1.—*Important strawberry varieties grown in the United States*

Rank	Variety	Total acreage	Origin [1]	Approximate date introduced (i) or originated (o)
		Percent		
1	Klondike	30.0	Br-Pri	1890 (o).
2	Howard 17 (Premier)	16.0	Br-Pri	1918 (i).
3	Aroma	10.0	Br-Pri	1889 (o).
4	Blakemore	8.0	Br-Pub	1923 (o).
5	Missionary	7.0	Ch	1900 (o).
6	Marshall	7.0	Ch	1890 (o).
7	Dunlap	3.5	Br-Pri	1890 (o).
8	Chesapeake	2.0	Ch	1903 (o).
9	Joe	2.0	Br-Pri	1899 (i).
10	Dorsett	2.0	Br-Pub	1923 (o).
11	Aberdeen	1.0	Br-Pri	1909 (o).
12	Lupton	1.0	Br-Pri	1905 (o).
13	Heflin	1.0		1902 (i).
14	Gandy	1.0	Br	1885 (o).
15	Beaver	1.0	Br-Pri	
16	Nick Ohmer	1.0	Br-Pri	1898 (i).
17	Redheart	.5	Br-Pri	1931 (o).
18	Belt (Wm. Belt)	.5	Br-Pri	1888 (o).
19	Mastodon	.5	Br-Pri	1917 (o).
20	Parsons (Pocomoke)	.5	Ch	1890 (o).
	Other varieties	4.0		

[1] Br=breeding; Pri=private agency; Pub=public agency; Ch=chance seedling.

The varieties now used probably represent better adaptation to conditions in the regions where they are grown than former sorts. Varieties such as Missionary, Klondike, Dunlap, and Heflin are more like the wild meadow strawberry of eastern North America than like the beach strawberry. Through the hundred years of evolution in the cultivated strawberry the varieties have been tending toward the native eastern wild strawberry. This has occurred because (1) most varieties have originated in the East; (2) seedlings with more of the characteristics of native wild strawberry have naturally succeeded best and have been selected by breeders; and (3) many varieties, such as Missionary, were found in the wild as chance seedlings. The latter may have originated either from seed of cultivated varieties or as the result of bees carrying pollen of cultivated sorts to the native strawberry. In some regions along the Atlantic coast most of the strawberries found growing wild are now in part derived from cultivated sorts. Natural crossing of cultivated with the beach and the Rocky Mountain strawberries has already started in the Western States, and many natural crosses have been found there.

Fairfax, of the eastern varieties, and Ettersburg 80 and 121, of the western varieties, are the nearest to an intermediate between the eastern meadow strawberry and the beach strawberry. Dorsett (fig.

5), Howard 17, Chesapeake, and Marshall are thinner leaved and thus somewhat closer to the Missionary, Klondike, and Dunlap group. The success of Etter (*8*) and Georgeson (*30*) whose work will be discussed later, in using selections of the beach strawberry has revived interest in this species. It is now being used extensively, particularly in the California and the United States Department of Agriculture breeding work, to increase vigor and to obtain resistance to root rots. Hybrids of cultivated varieties with *Fragaria chiloensis*, the beach strawberry, have much greater vigor than most variety crosses. It

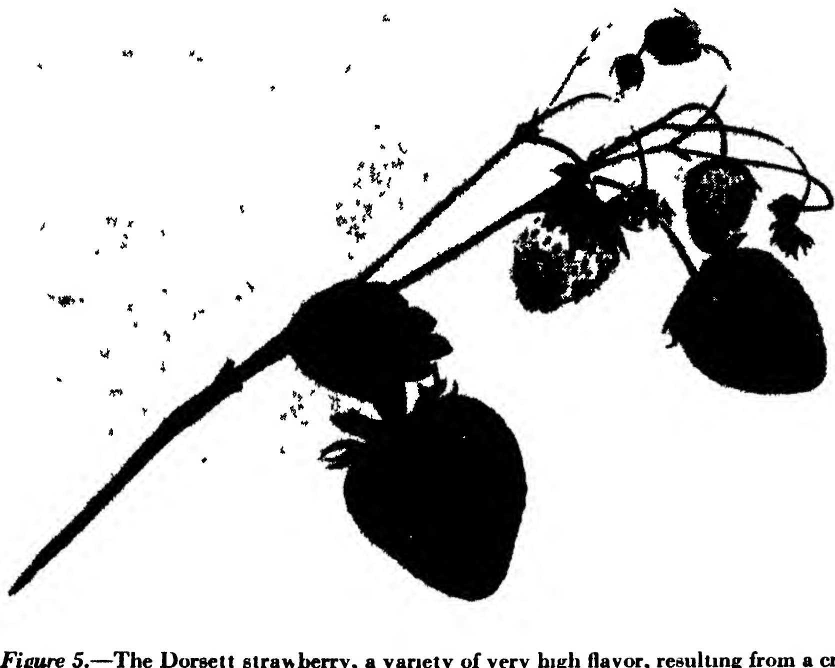

Figure 5.—The Dorsett strawberry, a variety of very high flavor, resulting from a cross of Howard 17, which is the principal variety of the northeastern United States, and Royal Sovereign, long the standard of excellence in northern Europe.

appears that through the scores of years since the strawberry came back from Europe some inbreeding has occurred that has lessened the vigor of the cultivated strawberry.

Important Varieties in Foreign Countries

The strawberries of Canada are similar to those of the United States, the varieties being the same in most instances. In eastern Canada, Dunlap, Parsons, Howard 17, and Glen Mary are the chief sorts. In British Columbia, British Sovereign, Magoon, Marshall, and Sir Joseph Paxton are raised in the milder coast climate, and Dunlap, Glen Mary, and Parsons (Gibson) in the interior.

Because wild parental types of the cultivated strawberry are not native to Europe, Asia, Africa, or Australasia, varieties of these countries are all, or nearly all, the result of breeding. The varieties so

developed differ from one another more than do American sorts. The principal varieties grown in each country are as follows:

England.—Royal Sovereign, Mme. Lefèbre, Late Leopold, Oberschlesien, and Huxley (probably Ettersburg 80). The Duke, Sir Joseph Paxton, Bedford Champion, and Mme. Kooi are being grown somewhat, and Western Queen and Pillnitz are being tested.

Scotland.—Scarlet Queen, John Ruskin, Royal Sovereign, MacMahon, and The Duke.

Germany.—Deutsch Evern and Noble for early, Sieger, Oberschlesien, and Roter Elefant for midseason, and Jucunda and Leopold for late. Vierlanden is raised near Hamburg.

Netherlands.—Jucunda, Deutsch Evern, and Noble, with some Scarlet and Oberschlesien.

France.—Minerve, Souveraine, Moutot, V. H. de'Thury, Dr. Morere, Paxton, Tomate, Marguerite, Leopold, and others.

Norway.—Deutsch Evern, Abundance, and Bedford Champion.

New Zealand.—Marguerite, Melba, Ettersburg (80 or 121?), Captain Cook, Noble, Helenslea, Surprise, and Royal Sovereign.

Victoria.—Melba and Wilson's Pride.

Tasmania.—Ettersburg (80 or 121?), Royal Sovereign, Melba, and Abundance.

STRAWBERRIES FROM SEED

The varieties of cultivated strawberries of the United States do not come true from seed. If 1,000 seeds of Marshall or Klondike or Howard 17 are planted, no 2 seedlings will be exactly alike. Some plants will be weak, some strong; some will make few runners, some many; some will have large fruit, some small; some will be productive, some unproductive. Out of the thousand, few if any will be as good as the parent. Because they do not come true from seed, and because they are so easily propagated by runners that root at the tip to form a new plant, all American varieties are propagated in this way, never by seed.

In Europe there are a few cultivated varieties called alpines or everbearing wood strawberries, some of which are often and others of which are always raised from seed. They produce much smaller fruit than do our cultivated varieties and are closely related to the wood strawberries of North America. Thus, the Bush White is an alpine variety that makes no runners, has small, white fruit, and, because it makes no runners, is always raised from seed. The Belle de Meaux is an alpine that produces runners, has red fruit, and may be raised from seed or propagated by runners. Such varieties have been selected, as have vegetables and other seed-propagated plants, until they come approximately true from seed. Seed varieties of alpines are relatively easy to establish as compared with seed varieties of the common cultivated strawberry. However, these alpine varieties are rarely grown in the United States.

Though it is extremely unlikely that any one of 1,000 seedlings of Marshall, Klondike, or Howard 17 will be better than its parent, breeders have learned that if Marshall is crossed with some other variety and 1,000 seedlings are raised, the progeny will be far more vigorous and productive than seedlings of Marshall that are not the result of crossing. Thus, from a cross between Marshall and Howard 17, Slate, at the New York (State) Agricultural Experiment Station, raised 1,132 seedlings and saved over 150 as especially promising (*55*).

From these he selected a seedling that he named Catskill, which combines many of the good qualities of both parents. It is now widely grown.

FLOWER TYPES IN STRAWBERRIES

Cultivated strawberries produce two general types of flowers—pistillate, and perfect or hermaphrodite (*11, 18*). Pistillate flowers contain pistils, the female parts, but no stamens, while perfect or hermaphrodite flowers contain both pistils and stamens, the male parts. The other two types of plants, staminate and that with both pistillate and perfect flowers on the same plants, are rare. Pollen is

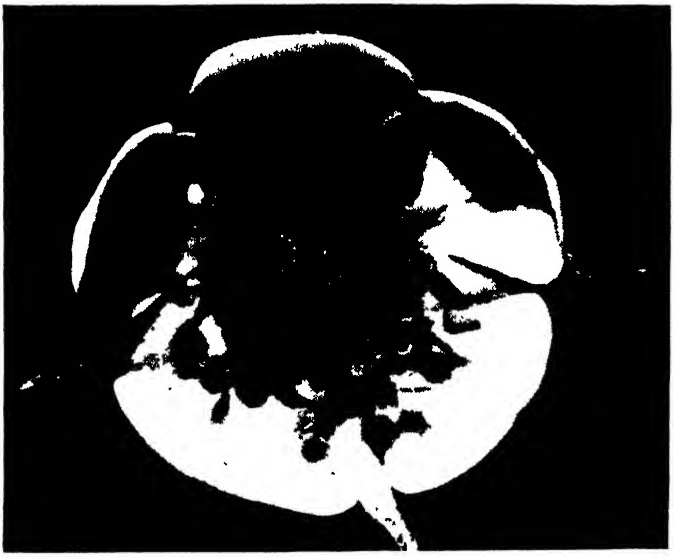

Figure 6.—A strawberry flower showing the pistils in the center surrounded by stamens. The anthers at the ends of the stamens are cracking open around the edges and shedding pollen.

carried by bees and other insects, but it is also thrown out of the stamens as the anthers crack open (fig. 6), or it is jarred out and blown by the wind and falls on the pistils. A variety having perfect or hermaphrodite flowers can produce fruit when planted by itself, but one with pistillate flowers cannot set fruit unless perfect-flowered plants are nearby to furnish pollen through the agency of bees or other insects. Because of this, varieties having pistillate flowers are not generally so desirable as those having perfect flowers, and few of them are grown now. However, some of these pistillate varieties are very productive. Pistillate varieties are also injured less by the strawberry bud weevil than perfect sorts, since this insect feeds on pollen; and in regions where it is serious, pistillate sorts are still grown. When the plants are in flower it is very easy to tell a pistillate from a perfect-flowered variety, as illustrated in figure 7.

Partial Sterility of Perfect-Flowered Varieties

Though the flowers of pistillate varieties nearly always set fruit when pollinated, those of perfect-flowered varieties rarely all set fruit. The flower may appear to be normal, but the pistils may be sterile. Under some conditions not 1 in 50 of the flowers of certain varieties sets fruit. Studies by Valleau (*60*) have shown that only the pistillate plants of the wild meadow, beach, and mountain strawberries set fruit. Perfect-flowered plants in the wild are in reality males, even though the pistils usually appear normal. Occasionally the first flower to open on a wild perfect-flowered plant may set a berry, and very, very rarely

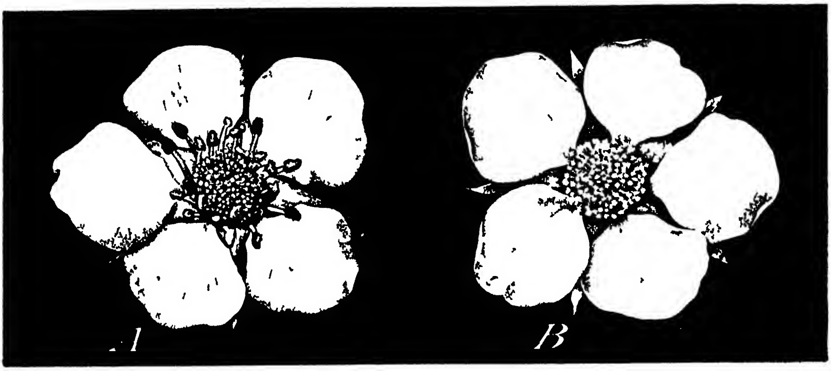

Figure 7.—A perfect or hermaphrodite strawberry flower (*A*) having both pistils and stamens, and a pistillate flower (*B*) having pistils but no stamens. Pistillate varieties will not produce fruit unless they are grown near plants having perfect or pollen-producing blossoms so that bees can carry the pollen to the pistillate flowers.

most of the perfect flowers on a plant of the wild meadow strawberry may set fruit.

The first flowers to open on a cluster of a perfect-flowered variety are more likely to set fruit than the later ones, and the last ones to open are most often sterile. On the average about one-third of the blossoms of cultivated perfect-flowered varieties are sterile. The clusters produced by the main crown of a plant have fewer sterile flowers than the later-formed clusters of branch crowns. Through scores of years, by breeding and selection, perfect-flowered varieties have now been obtained that set nearly all their flowers. In fact, under favorable conditions all the flowers of the Rockhill everbearing seem to set.

At its base the pistil contains a minute egg cell ready for fertilization when the flower opens. After pollen is placed on the end of the pistil, one or many of the pollen grains start to grow a tube down the center of the pistil. The pollen absorbs food from the tissues of the pistil, and finally one pollen tube reaches the egg cell. The sperm nucleus, a minute globular mass in the pollen grain, passes down the pollen tube, enters the egg cell, and unites with the egg nucleus. When the nuclei of the pollen and egg unite they form a single cell that is the germ of a new plant. By successive divisions of this original cell, the

embryo plant, contained in the seed that we see on the outside of the strawberry, is finally formed. Within a few hours after the pollen and egg nuclei unite, the ends of the pistils dry up. If no pollen reaches the ends of the pistils they will not dry up nearly so quickly. After the embryo has started to grow, the tissue around the seed starts to develop into what we call the strawberry. If any pistil is not pollinated, then the tissue around the base of that pistil does not develop. When the pistils on one side or part of a flower have not been pollinated or have been damaged by frost, the result is a misshapen berry.

TECHNIQUE OF BREEDING STRAWBERRIES (*19, 20*)

Crossing of strawberries may be done in the field under cages of wire screen or cloth or under sun traps (fig. 8, *A*). Making large numbers of crosses in the field is very laborious and must be done within a short time. Flowers may be killed by unseasonable late frosts, so that the work has to be repeated and time is lost. For these reasons, if facilities are available the crossing should be done in greenhouses, either heated or unheated (fig. 8, *B*).

The other advantages of using an unheated greenhouse are that (1) the flowers open about a month earlier than in the field; (2) it is possible to stand erect or sit while doing the crossing; (3) the pots can be carried to different parts of the greenhouse to save time; (4) insects usually do not interfere, so that the plants do not need to be covered; (5) the stamens do not open before the petals unfold, which makes it possible to emasculate and pollinate at the same time, while many stamens shed pollen before the flowers open out of doors; and (6) many perfect-flowered varieties produce primary, secondary, and even tertiary flowers having no pollen-bearing stamens, so that emasculation of such flowers is unnecessary, yet out of doors most flowers of the same varieties produce good stamens. Plants may be potted any time during the fall or winter for bringing into such an unheated greenhouse.

Pollination

In emasculating, the thumbnail is generally used to cut away the stamens, corolla, and calyx at one operation (fig. 9, *A*). If this is done with ordinary care, no injury to the pistils follows. Often the calyx and corolla are removed to identify crossed flowers even though emasculation is not necessary. The primary and secondary flowers, the first and second to open, contain far more pistils than the flowers opening later in a cluster. Berries developing from the primary and secondary flowers can set far more seed than the later berries, hence every effort is made to pollinate the earliest flowers on each cluster.

In crossing, the flowers having unopened pollen-bearing stamens are picked and allowed to wilt until the anthers crack open to let the pollen out. The flowers are used directly on those to be crossed, being held so that the stamens touch the pistils. The flower is then twirled by its stem so as to cover all the ends of the pistils with pollen (fig. 9, *B*). A flower with abundant pollen may be used to pollinate four

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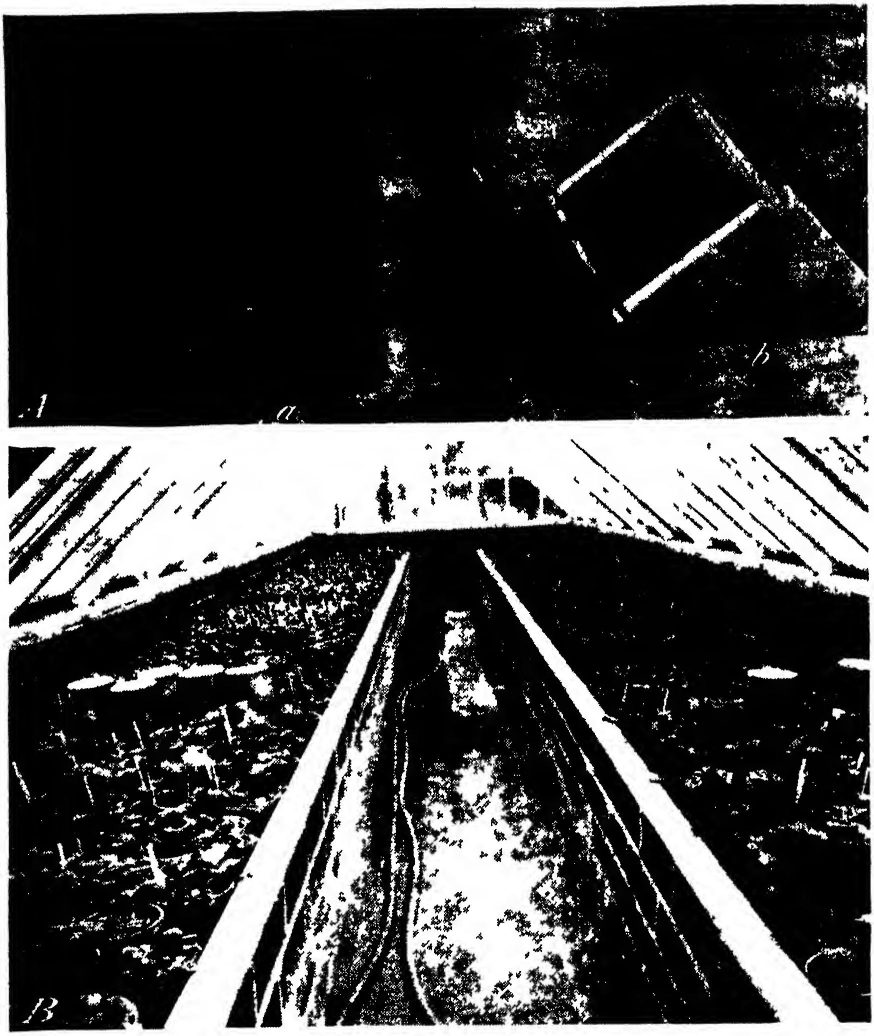

Figure 8.—*A*, Types of coverings formerly used to keep insects away from flowers that were being crossed in the field: *a*, A wire screen cage; *b*, a glass sun trap. In recent years the work has been done far more quickly and safely in cold greenhouses or propagating houses, as shown in *B*. *B*, Interior of a cold greenhouse at the breeding season. Note that the benches are of solid earth and that the center walk is below the ground level. The house is of the simplest construction, being made of coldframe sash. The potted plants of the different varieties to be used in breeding have started spring growth, and most of the crossing can be done before the flowers start on plants out of doors.

to six flowers or even more. Some breeders collect pollen and then use small brushes to apply it.

After being pollinated, the flower, flower cluster, or plant is marked to indicate the cross (fig. 10) and then bagged or protected in some

Figure 9.—Crossing the strawberry: *A*, Flowers being prepared for crossing. The petals, sepals, and stamens are removed by cutting them off with the thumbnail. *B*, Flowers being pollinated. The flower of the variety to be used as a male parent is being pressed against the pistils and the flower twirled between the fingers to brush the pollen onto the pistils.

way from insects if necessary (fig. 8, *A*). The berries are picked as soon as they are fully mature. The fresh berries may be mashed in dry sand to separate the seed, and the mixture of seed, pulp, and sand is sowed in flats and pots at once They are then covered with about one-eighth of an inch of sand, and at no time is the seed allowed to become dry. With temperatures from 60° to 80° F., the seed germinates in a few days. With very high temperature the seed may become dormant and stay dormant until after a period of cold weather. Soil to which commercial fertilizer has been added should not be used, for it may prevent germination.

Figure 10.—A pistillate variety used in breeding. The petals and sepals were removed from the flowers when they were pollinated in order to identify them. The label indicates that all 24 flowers were pollinated with U. S. D. A. selection no. 632 (Redheart).

Handling the Seedlings

When they reach a size convenient for handling (fig. 11), the seedlings are pricked either into flats 2 inches apart or into thumb pots. As soon as they are large enough (2 to 4 weeks) they are set in the field. If set in the field in Maryland by July 1 they should produce a good crop the next spring. The plants may be set 4 to 5 feet apart and allowed to make a small mat of runner plants, or 12 to 18 inches apart in the row and all runners kept off.

Selection of Seedlings

At the beginning of the ripening season, all plants that would not be desirable commercially, including dwarfs and those subject to leaf or root diseases, may be cut out. Further selection when fruit characters are judged will then be easier. The number of selections made for future testing varies greatly but is rarely over 10 percent and is usually less than 2 percent of the plants fruited (fig. 12). The

selections are then propagated and a second test on a larger scale, either a 25- or a 50-foot row, is made in comparison with standard varieties. After the second test some selections may be tested further for some special quality such as suitability for preserving, canning, or shipping, or for behavior in different regions of the country.

STRAWBERRY BREEDING IN THE UNITED STATES

Objectives

THE FINE dessert quality and the extensive cultivation of the strawberry today are a tribute to the ability and industry of breeders of

Figure 11.—Strawberry plants grown from seed. The five seedlings at the left are the proper size for repotting; the one at the right is larger than the usual size.

the past century and a half. Further improvement may consist largely in obtaining varieties with (1) greater resistance to leaf, crown, and root diseases, to the virus diseases, and possibly to insects and nemas (eelworms); (2) greater resistance to high and low temperatures and to drought; (3) better adaptation to long and short days (*17*); (4) better dessert quality under adverse weather conditions; (5) increased firmness and toughness of skin; and (6) better adaptation to specific uses such as deep red, firm, tart varieties for canning; varieties holding their shape, texture, flavor, and color after freezing; light red but red to the center, tart, firm ones for preserving (*15*); varieties with aroma suitable for flavoring, etc. Such improvements would lessen the risks now faced in growing strawberries. Varieties most desirable for freezing for the small-package trade have been found too subject to diseases or not productive enough to become commercial sorts. Southern varieties have been highly acid and without much aroma in cold and unfavorable weather, yet there are varieties that have high flavor under such conditions.

Methods of Breeding

So far, improvement has come through direct crossing of varieties and species and backcrossing to the parents. Crossing and the raising of large numbers of seedlings is relatively easy and has been a rapid and effective method of breeding. Backcrossing a seedling to one of its parents has long been used by strawberry breeders as a regular practice. There is much that can probably still by done by these methods. However, with new problems, new methods, and new

Figure 12.—After "Judgment Day" in the strawberry field. This photograph shows what is left after selection has been completed. The seedlings that have been found wanting have been destroyed, and of the thousands of plants originally in the field only a few remain.

facilities, plant-breeding practices may change. The sporting of Blakemore, Howard 17, and other varieties to yellow plants may make new methods useful.[4] Sporting to yellow leaves seems to be due to the appearance of recessive characters. Because this yellow plant is worthless, a method needs to be devised for eliminating its inheritance from breeding stock and from varieties to be introduced.

The use of selfing to obtain relatively pure lines has not been satisfactorily explored, though some selfing has been done by several breeders. When selfing has proceeded for two or three generations, the plants are not vigorous and may be easily lost. Only under very favorable conditions can they be kept alive. For this reason, little information on this method is yet available. Yet immunity from or high resistance to leaf spot or other diseases may be due to recessive

[4] Darrow, G. M Notes on variegated leaf troubles of strawberries U S Bur Plant Indus Plant Disease Reptr 18 26-29 1934

genes and appear only after inbreeding. Yellow leaf seems to be a recessive character that might be eliminated by selfing and by selecting selfed lines that do not carry it.

Private Breeders

Of the private breeders who produced varieties previously listed, the following are still living: A. F. Etter, Ettersburg, Calif., originator of Ettersburg 121 and other varieties; E. C. Howard, Belchertown, Mass., who was associated with his father in the origination of Howard 17 and Howard Supreme varieties; Harlow Rockhill, Conrad, Iowa, originator of Rockhill and Progressive, everbearing varieties; and Jeff Beaver & Son, Eau Claire, Wis., originators of Beaver. Other private breeders are Horace Wray, White Salmon, Wash., originator of Wray Red; and W. Kosuga, Sandy, Utah, originator of Berri Supreme.

These breeders made crosses and selected the seedlings that seemed to come nearest their ideal. Some of them have kept detailed records of their work, as the following parentage of Howard 17 shows:

$$\text{Howard 17}\left\{\begin{array}{l}\text{Seedling no. 1 of Howard}\left\{\begin{array}{l}\text{Seedling no. 4 of Howard}\left\{\begin{array}{l}\text{Haverland}\\ \text{Belmont}\end{array}\right.\\ \text{Clyde}\end{array}\right.\\ \text{Crescent}\end{array}\right.$$

The Howards tried to recombine in one variety the desirable qualities in several. Slate (*55*) has stated that Howard 17 is the outstanding parent used at the New York station. It has also been an exceptional parent in the breeding work of the United States Department of Agriculture.

A. F. Etter (fig. 13) has collected and used selected wild strawberries in his breeding work, which began about 1885 (*8*). His most valuable contribution has been this use of selections from the wild. Most of the 50 or more varieties introduced by him are derived from selections of the beach strawberry, *Fragaria chiloensis*, crossed with cultivated varieties. Qualities that he has bred into strawberry varieties through use of selections of the beach strawberry are being extensively used by other breeders. Thus, Redheart is a cross of Portia × Euresko, the latter being one of Etter's varieties. Southland resulted from a cross of Howard 17 × Ettersburg 80, while Corvallis is a cross of Marshall × Ettersburg 121. Many selections at experiment stations resulting from breeding work and under test at present have as one parent one of the Etter varieties or a variety or selection derived in part from his varieties.

Harlow Rockhill began his work with the everbearing strawberries in 1895 and has used both American and European sorts in his breeding. Progressive was his first production to be widely grown. His later variety, Rockhill (Wayzata), is resistant to cold and to leaf diseases and is one of the highest in dessert quality in the United States (fig. 14).

Federal Strawberry-Breeding Work

The Federal strawberry-breeding work (*19*, *20*) has been carried on in Maryland since 1920. The work was extended in 1928 to include cooperative work at the North Carolina Coastal Plain Branch Station at Willard and the Oregon Agricultural Experiment Station at Corvallis.

Over 86,000 seedlings, representing hundreds of crosses, have been fruited at Glenn Dale, Md., and at United States Horticultural Station, National Agricultural Research Center, Beltsville, Md. In all, over 150 varieties and 20 selections of species have been used in this breeding work. Selections to the number of 1,999 have been made, 7 varieties have been named and introduced, while 342 selections are still unnamed and are being held for further testing or for breeding.

The first work at Willard consisted of tests of selections from the Glenn Dale station. Beginning in 1929, small seedlings raised in Maryland were taken to Willard and fruited there. Since the beginning about 54,000 seedlings have been grown at Willard and 1,245 selections have been made. No selections have been named, though several are being extensively tested and propagated. The crosses have been made especially to obtain firmer, higher flavored shipping varieties for the South.

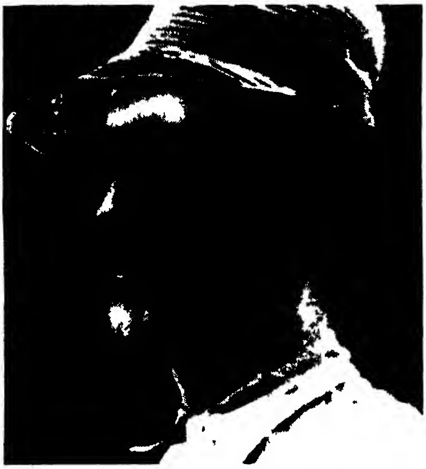

Figure 13.—A. F. Etter, Ettersburg, Calif., pioneer in the use of native western strawberries, plums, apples, and gooseberries. Not only have his varieties been widely grown, but other breeders have used them extensively in their breeding work.

At the Oregon station the first work also consisted of tests of selections made in Maryland. However, crossing was immediately begun, and to date some 97,000 seedlings have been fruited and 1,331 selections made. No selections have yet been named, though many are being extensively tested. The crosses made have been largely to obtain better preserving, freezing, canning, and shipping berries.

At the United States Horticultural Field Station, Cheyenne, Wyo., the first selections of the wild Rocky Mountain strawberry, *Fragaria cuneifolia* Nutt., were made in 1935. Though small fruited, they proved much hardier than cultivated varieties, and in 1936 over 30,000 plants were collected, chiefly from the States of Wyoming, Colorado, Utah, Montana, and South Dakota. Selections of these are to be used by Powers and Hildreth in crossing to produce varieties more resistant to cold, dry winters.

Extensive tests of many of the selections at Willard, N. C., have been made in Maryland and at Corvallis, Oreg., to find some especially adapted to freezing in small packages with sugar or sirup. Similar tests have been made of the preserving and canning qualities of many varieties. As a result of this work, the Blakemore was selected early in the breeding work for its superior qualities for the making of preserves (*15*). It is considered the best of all varieties for this purpose in the United States. The Redheart was selected for its canning qualities and is now raised more extensively than any other canning variety. Breeding for firmness and adaptation to short day

length requirements at the Willard station have been other objectives Some of the crosses that have some of these desirable qualities are listed in the appendix under Sources of Superior Qualities in Strawberries

Studies on the sterility of flowers (*12*), types of flower clusters (*13*), number and length of runners, stomata of the leaves (*14*), transpiration from the leaves, fruit-bud development (*6*), spacing of plants, and leaf area in the late fall have shown just what plant characteristics are most desirable and why. Thus, the fertility of all the flowers of Rockhill, the low-branching fruit clusters and early fruit-bud initiation

Figure 14.—The Rockhill everbearing variety (*A*) contrasted with a variety of the Alpine everbearing (*Fragaria vesca semperflorens*) (*B*). Note the much smaller fruit of the latter.

of Howard 17, the long, large runner and natural spacing of plants of Fairfax, the type of stomata of Blakemore (*14*), and the extensive leaf area of Dorsett when spaced—these have been found to be desirable characteristics under some conditions and useful in breeding. In fact, an intimate and extensive knowledge of such characteristics in varieties is of great importance in selecting varieties for breeding and in making selections from seedling fields.

Strawberry Breeding at State Experiment Stations

Extensive strawberry breeding is a part of the work at many State experiment stations. A list of the workers at these stations and the locations of their work is given in the appendix.

A relatively small part of the total strawberry acreage of the country—about 10 percent—consists of varieties originated by public

agencies. However, the acreage of Catskill, Dorsett, Fairfax, and other new introductions is increasing rapidly, and these varieties are becoming important commercial sorts. Strawberry breeding has been started only recently at many experiment stations as the need for better varieties has become apparent. Results from much of this work are not yet, of course, in the trade.

Alaska

Strawberry breeding was begun in Alaska (*30*) in 1905, the first crosses being made between cultivated varieties and selections of the beach strawberry, *Fragaria chiloensis*. Later, selections of the hardy interior wild strawberry, *F. cuneifolia* (*F. platypetala* Rydb.), as well as numbered seedlings, were also used in crossing. Named varieties from the States do not succeed in the climate of Alaska, and crosses were made to obtain varieties with the size and productiveness of the cultivated varieties and the hardiness of the native wild strawberries. Some of the resulting hybrids were found to be hardy at Fairbanks, in the interior of Alaska, where extremely low temperatures occur in winter and where there is continuous daylight for about 2 months in summer. Up to 1922 some 11,600 seedlings had been raised. As a result of this breeding work strawberries are now commonly grown in Alaska. Since about 1922, varieties originating at the experiment station at Sitka have supplied the markets both on the coast and in the interior, even above the Arctic Circle.

Minnesota

Strawberry breeding in Minnesota was begun in 1908 and has continued to the present. The earlier work consisted of crosses between commercial varieties to obtain hardier sorts. Between 75,000 and 100,000 seedlings were raised from 1909 to 1924. Seven varieties were named and introduced as the result of this work—Duluth and Deephaven as everbearing sorts, and Minnesota, Minnehaha, Chaska, Easypicker, and Nokomis as early summer sorts. The principal varieties used as parents were Abington, Autumn, Beder Wood, Brandywine, Clyde, Crescent(?), Duluth, Dunlap, Easypicker, Enhance, Golden Gate, Jessie, Margaret, Pan American, Prolific, and Sheppard. Similar work on a smaller scale has been continued since 1927.

Selection within self-fertilized lines was begun in 1922 and is being continued. Varieties selected for desirable characters are self-pollinated, about 5 percent of the better seedlings propagated, compared, and the superior lines again selfed. Lines that have been selfed for one, two, and three generations are now being grown. The principal varieties used in this work are Belt, Chaska, Dunlap, Howard 17, Marshall, and Minnehaha, and to some extent Beaver, Duluth, Early Bird, Mastodon, Minnesota, and Progressive.

South Dakota

The breeding work in South Dakota (*31*) has consisted of an attempt to introduce into the cultivated strawberry the hardiness of the native strawberry of the Dakotas. Dakota No. 1 and Dakota No. 2 were

introduced, and the former, now known as Dakota, is perhaps the hardiest variety known in the United States.

California

The breeding work in California was begun by W. T. Horne and A. G. Plakidas in 1925–26 to obtain varieties resistant to the yellows or xanthosis virus disease. In recent years the work has been carried on by E. V. Goldsmith and H. E. Thomas, and resistance to phytophthora root rot has been made a second major objective. Varieties and selections obtained from A. F. Etter and the United States Department of Agriculture, as well as many commercial varieties, have been extensively used. Among the desirable characters for California conditions not necessarily considered elsewhere are longevity of plant, open crowns, long inflorescences, small seeds, and heavy production in spring, summer, and fall. The work has centered at San Jose until recently, when part of it was transferred to Davis. Though very large numbers of seedlings have been raised and many selections made, no varieties have yet been named and introduced.

New Jersey

Breeding work at the New Jersey Agricultural Experiment Station (*7*) was begun in 1928 and has continued to the present. All available varieties having promise for New Jersey conditions, as well as many unnamed selections from other institutions carrying on strawberry breeding, have been tested. The principal varieties used include Aberdeen, Berri Supreme, Bliss, Bouquet, Chesapeake, Dorsett, Fairfax, Gandy, Howard 17, Lupton, Mastodon, Parcell, Pearl, Redheart, Teddy Roosevelt, Wyona, and U. S. D. A. 854 and 875. Besides published data on inheritance of earliness and lateness, data have been obtained on sex ratios, shape, color, flavor, and firmness of berry, and on inheritance of the everbearing characteristic. One variety, N. J. 35, was introduced in 1936. Lupton transmitted its size and attractiveness but also its poor quality to its seedlings. Chesapeake transmitted its good flavor and its unproductiveness. Many of the best very late ripening seedlings have had Pearl as one parent. Fairfax seedlings have had high flavor and were exceptionally firm.

New York

Strawberry breeding at the New York station at Geneva was begun in 1889 by C. J. Hunn and has been continued at intervals ever since (*1*, *2*, *54*). At least 68 named varieties, as well as many selections from crosses, have been used in the breeding work. Over 13,000 seedlings have been raised and 21 varieties have been introduced. Several of the more recent introductions are grown to a slight extent, chiefly in New York State. Clermont is grown to a considerable extent in Erie and Oswego Counties. Catskill, however, is rapidly becoming an important commercial variety from Maryland to Missouri and northward. Most of the introduced varieties have had Marshall or Howard 17 or both as a parent, Marshall contributing high flavor and large size of berry, and Howard 17 productiveness and disease resistance. In a summary of the best parents in the breeding work, the importance of Howard 17 as a parent is emphasized.

A large percentage of its seedlings produce very smooth, uniform-shaped, glossy berries that hold up well to the end of the season. A few selections of species have been used in crosses.

Connecticut

At the Connecticut station, Howard 17, Chesapeake, and Glen Mary were inbred for three generations and then the F_3 (third-generation) progeny were crossed. The strawberry was reported to respond to inbreeding and crossing in much the same way as corn. The F_3 plants were dwarfed, but crossing seemed to bring back the vigor that the varieties originally possessed. From about 9,000 seedlings that resulted from crossing the F_3, promising selections have been made and are being given field trials in different sections.

Other State Stations

At the Maine station, breeding work was begun in 1934 to obtain better late varieties. At the Massachusetts station, breeding work was also begun in 1934 to obtain late varieties of better dessert quality and also better pistillate sorts.

In Illinois, breeding work to obtain varieties resistant to brown stele root rot was started in 1935. Mastodon, Aberdeen, and Redheart, which appear resistant, have been used in crossing.

In Wisconsin, breeding was begun in 1933 to obtain productive early and late commercial sorts. Howard 17, Beaver, Corvallis, and Vanguard have been used as parents.

In Missouri, though some crossing was done at the Mountain Grove station in 1902 and 1919, no varieties were introduced. In 1936 selections of the meadow strawberry, *Fragaria virginiana*, were crossed with Aroma, Blakemore, Fairfax, Dorsett, Chesapeake, Howard 17, and Joe, to obtain varieties with the resistance to cold, drought, and disease, and the high flavor of the wild strawberry.

In North Dakota, small-fruit breeding began in 1920 and has continued to the present. The Dry Weather variety, resistant to drought, was introduced in 1928. Resistance to winter cold, summer heat, and drought is being emphasized.

In Tennessee, strawberry breeding began in 1923 and has continued to the present. Both selfing and crossing have been carried on to obtain productive varieties hardy in summer, resistant to leaf and root-rot diseases, and with attractive, firm, high-flavored berries suitable for processing and shipping. Some selfed seedlings of Aroma were found to be notably vigorous and productive.

At the Louisiana station breeding work has recently started with the objective of producing varieties resistant to leaf spot and scorch, of good shipping qualities, and sweeter than Klondike.

In Texas breeding work began in 1933 to obtain varieties resistant to heat, drought, and leaf spot, and that would produce sufficient runners under the climatic conditions of southern Texas.

In Washington State, at Puyallup, strawberry breeding was begun in 1929 and has been continued to the present. The objectives have been firm- and soft-fruited, high- and low-yielding, and red- and light-fleshed varieties.

In Oregon, at Corvallis, breeding work has been carried on in cooperation with the Federal work since 1928. Previously, however, the Corvallis variety was originated by C. E. Schuster from a cross between Marshall and Ettersburg 121. Schuster noted that Ettersburg 121 transmitted its vegetative characteristics with remarkable uniformity.

STRAWBERRY BREEDING IN OTHER COUNTRIES [5]

Canada

The Central Experimental Farm of the Dominion of Canada at Ottawa and several of the provincial experiment stations, notably the Ontario Horticultural Experiment Station at Vineland, have carried on strawberry breeding more or less continuously for many years. Several recent selections made at Ottawa are being extensively tested (*21*). At Vineland some 30,000 seedlings of 300 crosses and 60 open and self pollinations were raised, 340 selections were made, and several named (*59*). Two, Vanguard and Vanduke, were grown to some extent at one time.

England

Among private breeders in England, the firm of Laxton Bros., at Bedford, has been prominent for its berry breeding for over 50 years, and the varieties of strawberries originated by the firm have long been important in Great Britain as well as on the continent of Europe, in Australasia, and in other parts of the world. Among these, Noble, Royal Sovereign, Scarlet Queen, Leader, Fillbasket, The Laxton, Latest, Bedford Champion, and The Duke have been particularly important varieties. Royal Sovereign is one of the parents of Dorsett and Narcissa and possibly of Fairfax (*16*) also.

Strawberry breeding by public agencies in England is being carried on at the Long Ashton Research Station, University of Bristol, at the Horticultural Research Station at East Malling, Kent, and at the John Innes Horticultural Institution, Merton. The earliest work was that by C. W. Richardson from 1910 to 1922, on inheritance of characteristics in the species having seven pairs of chromosomes and to some extent in cultivated varieties. Spinks carried on rather extensive breeding work at the Long Ashton station. By 1923 some 5,000 seedlings had been raised and 145 selections made. He noted that Leopold transmitted its resistance to aphids, that seedlings of Leopold × Royal Sovereign and President × British Queen were susceptible to mildew, but that seedlings of Leopold × Stirling Castle were resistant to both aphids and mildew. All seedlings of V. H. de Thury × The Earl and L. Gautier × White Perpetual were resistant to mildew, and only 1 in 60 seedlings of V. H. de Thury × King George was susceptible. The seedlings of Bedford Champion × King George, Leader × St. Antoine, and Fillbasket × Bedford Champion were the best flavored.

Germany

In Germany three stations are carrying on breeding work with strawberries. At the University Institute for Fruit Culture, in

[5] Reports have been received from H. Wenholz, Sydney, New South Wales; W. S. Rogers, East Malling Kent, England; M. B. Davis, Ottawa, Canada; and W. S. Strong, Vineland, Ontario, Canada. Lists of the workers and of the varieties from foreign stations are given in the appendix.

Berlin, quick- and early-ripening varieties with not too many flowers are being bred for forcing houses. At the Kaiser Wilhelm Institute in Müncheberg the breeding of large, productive, high-flavored everbearers has been started, and studies are being made on methods used in making selections, on inheritance and correlations of different qualities, on sex ratios, and on the periodicity of the growth phases. At the Horticultural Station at Pillnitz, under the direction of Professor Schindler, productive, high-flavored varieties that hold their color, that are resistant to unfavorable weather conditions, and that ship well are the objectives. Six varieties have been named and introduced from this station.

Australia

At the Hawkesbury Agricultural College, New South Wales, breeding for resistance to diseases such as root rot and leaf scorch is a primary objective. Seedlings of *Fragaria chiloensis* × British Sovereign, Fendalcino × British Sovereign, and Southland × British Sovereign have shown the most promise.

SUPERIOR GERM PLASM

In the strawberry, as in other plants and in animals, superior germ plasm refers to one or more inheritable qualities that may be desirable or useful to the grower or consumer. Thus, a variety or a species with fine flavor, or resistance to disease or to extremes of high or low temperature, would be counted as having superior germ plasm in that respect. Certain characters would be considered undesirable; for example, the one-flowered cluster of *Fragaria daltoniana* J. Gay.

Both of the species from which the common cultivated varieties are derived, *F. virginiana* and *F. chiloensis*, as well as *F. cuneifolia*, are extremely variable in the wild. Cultivated varieties, therefore, have various combinations of characters, desirable as well as undesirable. In general, the scarlet color, high aroma, tart flavor, and wide adaptation to climatic and soil conditions in cultivated varieties are derived from *F. virginiana*. The history of the strawberry and the success of Etter and Georgeson, who have used new selections of *F. chiloensis*, indicate that there may be many desirable characters in the wild forms of this species that have not yet been used. Tests of selections of *F. cuneifolia* and of hybrids with it indicate cold and drought resistance, everbearingness, and quickness of response to warm spring temperatures in this species (figs. 15 and 16). These desirable qualities might extend both the range of cultivation and the fruiting season of strawberries. As yet the collections and tests of *F. cuneifolia* are too limited to fully evaluate these and other qualities that it may have. However, hybrids of *F. cuneifolia* with cultivated varieties have made strawberry production possible even at Fairbanks, Alaska (*30*).

Because native species often are rather difficult to keep alive, crosses showing hybrid vigor may be useful in holding their superior germ plasm in breeding stock. *Fragaria chiloensis* is susceptible to cold injury in Maryland. Its hybrids with Fairfax and Blakemore are vigorous and are used as a source of the characters of *F. chiloensis* in the Federal breeding work. Because *F. cuneifolia* becomes everbearing at low elevations, it makes few runner plants, and for this

reason, too, hybrids serve as a source of its characters. Some of these hybrids and other selections having superior germ plasm are listed in the appendix.

Studies indicate that a variety or species showing any characteristic actually will transmit the character to a large proportion of its seedlings. Crosses of varieties and species, as well as genetic research, support the supposition that in the strawberry most qualities of importance in breeding are quantitatively inherited, that is, that there are genes for such qualities as flavor, color, size, firmness, etc., in each, or in many at least, of the eight homologous chromosomes

Figure 15.—The wild strawberry of the Rocky Mountains, *Fragaria cuneifolia.* So far it has been little used in breeding, but it is resistant to drought and cold and is everbearing when grown in Maryland.

(one pair in each four sets), and they have a cumulative effect. For example, it is as if the dark Redheart contained a gene for color in seven of the eight chromosomes, the less dark but still deep-red Dunlap in six of the eight, the medium-red Dorsett in five of the eight, the light-red Blakemore in four of the eight, and the White Sugar in about two of the eight. If Redheart is crossed with a dark-fruited variety, the seedlings are mostly dark-fruited; if it is crossed with a light-fruited variety, the seedlings are mostly intermediate.

In making crosses, therefore, breeders have learned that if a variety shows any desirable quality, in general that quality can be transferred to any other variety if a large enough number of seedlings (crosses between the two) are raised. Sometimes the seedlings nearest the ideal are backcrossed with one or the other parent before the desired character is obtained. The results published by Spinks (*57, 58*) and by Richardson (*50, 51*) in England indicate that it is easier to obtain many qualities in certain crosses than in others. Thus, Bedford Champion × King George V gave 80 productive seedlings out of 235,

while Royal Sovereign × King George V gave only 8 out of 114. Richardson obtained seedlings with the highest flavor from a cross of Filbert Pine × King of the Earlies. Until the genetic constitution of varieties is worked out, the location of superior germ plasm must be assumed to lie only in varieties that show it.

Because of the apparent quantitative inheritance of characters in the strawberry, a scoring system is used in the Federal breeding work to evaluate the qualities. A similar system was used by Keffer in Missouri in 1893. For flavor, color, firmness, resistance to leaf spot, resistance to leaf scorch, and vigor, seedlings are scored on a scale of

Figure 16.—Crosses of the Rocky Mountain strawberry, *Fragaria cuneifolia*, with the Marshall variety.

1 to 10, 1 representing best and 10 worst. Thus, at Beltsville, Md., Missionary might score 3 in resistance to leaf spot, Fairfax 1.5, Howard 17 also 1.5, Marshall about 8, and Beaver 8. For flavor, Dorsett would score 1, Howard 17 about 3, and Lupton 5. Richardson in England used such a scoring system for strawberries, although he used 1 as poor and 8 as finest in flavor. Since the vegetative cells of garden strawberries contain eight sets of chromosomes (seven to a set, $8 \times 7 = 56$ chromosomes), Richardson's scoring corresponds to the number of sets.

Though in years past it may not have seemed possible to have most of the desirable qualities of the strawberry in any one variety, it now seems practicable to get most qualities in breeding stocks and then cross these to obtain combinations of the qualities desirable for certain conditions. The history of the strawberry bears out this conclusion. Thus, the origination of the Wilson is considered to have made it possible to obtain varieties both firm-fruited and productive for different regions. The Howard 17 has added high resistance to diseases in Northern States to the superior germ plasm. Possibly within the next few years breeding stocks may have, in addition to

the fairly firm fruit, the productivity, and the disease resistance already obtained, (1) the cold-hardiness of the Progressive and of *Fragaria cuneifolia;* (2) the heat resistance of Missionary; (3) the drought resistance of *F. cuneifolia* and of U. S. D. A. 1791; (4) the smoothness of flesh of Corvallis; (5) the dessert quality of Rockhill in Minnesota and of Dorsett in Maryland; (6) the size of Marshall in the Pacific Northwest; and (7) the tough skin of Redheart. Later breeding may then add qualities for specific regions or uses, as the bright color of Blakemore for a preserving and shipping sort; the deep color of Redheart for a canning sort; the peculiar flavors—like grapes, apricots and red and black raspberries—of crosses of U. S. D. A. 652 for novelties; the short-day adaptation of the Missionary for Florida; the longer day adaptation of Howard 17 for other regions; and the everbearingness and runner production of Mastodon.

In Europe the source of superior germ plasm may also be indicated by the qualities for which outstanding varieties are known. Thus, British Queen and Dr. Hogg are considered to have the finest flavor, while Royal Sovereign and Paxton have the best flavor of the widely raised sorts; The Duke, an early, and Waterloo, a late variety, are often considered drought-resistant; Noble retains its color especially well in cooking and is one of the finest flavored and most widely adapted sorts; H. Vicomtesse de Thury (Stirling Castle), Deutsch Evern, and Little Scarlet are considered the best for jam and are very rich-flavored; Laxton's Latest, Late Leopold, Waterloo, and Givon's Prolific are very late sorts; Deutsch Evern and Royal Sovereign are superior forcing varieties; Mme. Kooi is very large and one of the most productive but is soft and of poor quality; Laxton's Latest is of the largest size; and Royal Sovereign, Sir Joseph Paxton, and Dr. Morere are widely grown, productive main-crop sorts, the Sir Joseph Paxton being frost-resistant. Late Leopold also escapes spring frosts. The Laxton grows where most other sorts do not succeed. Deutsch Evern is one of the best for preserving.

STRAWBERRY GENETICS AND CYTOLOGY [6]

There has been little satisfactory interpretation of the inheritance of characters in the strawberry, although there has been considerable study of the matter (*3, 4, 5, 6*). This is because most of the characters such as color, size, shape, and structure of berry are quantitative and determined by several genes. Three pairs of contrasting characters, however, are available for study.

Femaleness versus various degrees of hermaphroditeness has been extensively studied. In most cases when a hermaphrodite variety is selfed only hermaphrodite seedlings are obtained (*2, 9, 37*). Femaleness × hermaphroditeness gives in most cases at least a 1 to 1 ratio, apparently indicating a single pair of allelomorphs located in a single pair of chromosomes. However, hermaphroditic varieties and seedlings represent an unbroken series from complete fertility to complete sterility of the pistils, and a satisfactory genetic explanation is yet to be made. If the chromosome sets of the cultivated strawberry are not now identical, and if pairing takes place between chromosomes in different sets of seven, then more or less sterility would be expected.

[6] This section is written primarily for students or others professionally interested in breeding or genetics.

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The unbroken series from complete sterility to complete fertility indicates that random pairing between all the chromosomes of all four sets actually occurs.

A second pair of contrasting characters is June-bearing versus everbearing. Everbearing varieties × everbearing varieties gave at Ottawa, Canada, 85 everbearing to 66 June-bearing, while everbearing × June-bearing and June-bearing × everbearing gave 257 everbearing to 788 June-bearing. The everbearing varieties are evidently heterozygous and the June-bearing homozygous. Assuming that everbearingness is due to two dominant complementary genes, *A* and *B*, then the everbearing would have the composition *AaBb* and, selfed, would give a 9 to 7 ratio, which was found, 85 everbearing to 66 June-bearing. When June-bearing are crossed with everbearing, a 1 to 3 ratio would be expected, or 261 everbearing to 783 June-bearing, which is very close to the 257 everbearing and 788 June-bearing actually found.

In England, Richardson selfed both the everbearer St. Antoine de Padoue, getting 108 everbearing to 22 June-bearing, and the everbearer Laxton Perpetual, getting 69 everbearing to 11 June-bearing. When he crossed a June-bearing Bedford Champion with an everbearing Laxton Perpetual he got 24 everbearing to 53 June-bearing. One of these June-bearing F_1 plants, when selfed, gave 8 June-bearing to 6 everbearing. These numbers indicate (1) that his everbearers did not have the same genetic constitution as those at Ottawa, Canada, and (2) that more than two and probably four complementary genes were involved, or that, if there were only two genes for everbearingness, they were linked. However, too few numbers have been raised for definite conclusions.

A third set of contrasting characters may possibly be useful in studies on inheritance, namely, normal versus variegated or chlorotic leaves. Richardson and Clark have made some studies on their inheritance. However, enough records have not yet been secured to indicate the genetic composition of a variegated plant.

Strawberry Species of the World

Although about 150 species names have been applied to the strawberry, the most recent monograph (*42*) described but 45, a number that is undoubtedly much too large. This monograph lists 4 species for Europe, 26 for North America, 1 for South America, and 15 for Asia. However, many of these can hardly be separated from one another and a total of about eight includes all the distinctive species. These eight belong to three groups as follows:

Fragaria vesca (wood strawberry) group, 7 pairs of chromosomes:
1. *F. daltoniana* J. Gay, southern Asia.
2. *F. nilgerrensis* Schlecht., southern Asia.
3. *F. vesca* L., circumpolar.
   Variety *semperflorens* Duch., Alps.
   F. californica[7] Cham. and Schlecht., North America.
4. *F. viridis* Duch. (*F. collina* Ehrh.), central Europe.

Fragaria moschata (open wood strawberry) group, 21 pairs of chromosomes:
5. *F. moschata* Duch. (*F. elatior* Ehrh.), central Europe.

Fragaria virginiana (cultivated strawberry) group, 28 pairs of chromosomes:
6. *F. chiloensis* (L.) Duch., coast of Alaska to central California, southern Chile, mountains of Hawaii.
7. *F. cuneifolia* Nutt. (*F. platypetala* Rydb.), Rocky Mountains.
8. *F. virginiana* Duch., eastern North America.

[7] *Fragaria californica* is very close to *F. vesca* and may be considered only a botanical variety of *F. vesca*.

Though these eight may include all the wild species, a final classification must await extended field studies of Asiatic forms. Six of the species are illustrated in figures 17 and 18.

Species With Seven Pairs of Chromosomes

The first four species have seven pairs of chromosomes (*40, 62, 64*) and are in general smaller plants with thinner leaves and smaller fruit than American cultivated varieties. *Fragaria daltoniana*, *F. collina*, and *F. nilgerrensis* belong to the *F. vesca* group and so far have not appeared to have qualities of value for breeding. *F. daltoniana* is unproductive, since it has one-flowered flower clusters. The fruit of *F. collina* is very small, and the plants have not survived in Maryland. The berries of *F. nilgerrensis* are many-seeded and rather tasteless. The plant, however, is vigorous. A number of varieties of the everbearing *F. vesca* var. *semperflorens* are grown to some extent in Europe. Though the fruit is smaller than that of American cultivated sorts, it is aromatic and borne freely throughout the summer in the climatic conditions of northern Europe, but it has not been successful in the United States. The fruit of *F. vesca* and *F. californica* is small—too small to be worth while.

Varieties of *Fragaria moschata*, the open wood strawberry of Europe, which has 21 pairs of chromosomes, are cultivated to some extent in European gardens for their very aromatic vinous-flavored fruit. Though the fruit is small, it is larger than that of the alpines. Varieties like Royal Hautbois and Black Hautbois grow fairly well in the northern United States if protected in the winter, but they have never succeeded commercially. La Constante, a French variety supposedly derived from *F. chiloensis* × *virginiana*, is reported to have much of the vinous flavor of *F. moschata* and may possibly be a source of this flavor for breeders.

Species With 14 Pairs of Chromosomes

Species with 14 pairs of chromosomes have not been known in the wild until recently, when Fedorova (*27*) reported that Petroff found a form with 14 pairs of chromosomes, which he referred to as *Fragaria orientalis* A. Los. Los., an eastern Asiatic species formerly classified with botanical varieties of *F. vesca*. Longley has suggested that the ancestral strawberry from which the others descended was close to *F. vesca*. This has the basic number of 7 chromosomes in the germ cells (diploid number 14). Lilienfeld (*39, 40*) recently has apparently proved that *F. moschata* (*F. elatior*), which has 21 chromosomes in the germ cells (diploid number 42), actually was derived in ages past from species with 7 pairs of chromosomes. He reached this conclusion because, in crossing a species having 7 pairs of chromosomes with one having 21 pairs of chromosomes, 14 chromosomes of *F. moschata* paired with 14 from the *vesca* type, and 2 sets of 7 from *F. moschata* paired with 2 other sets just as though they were a 14-chromosome species. The resulting seedlings were fertile and constitute a new species with 14 pairs of chromosomes named by Lilienfeld *F. elnipponica* Lil. (derived from *F. elatior*, a synonym of *F. moschata*, and *F. nipponica* Mak., which is a Japanese form of

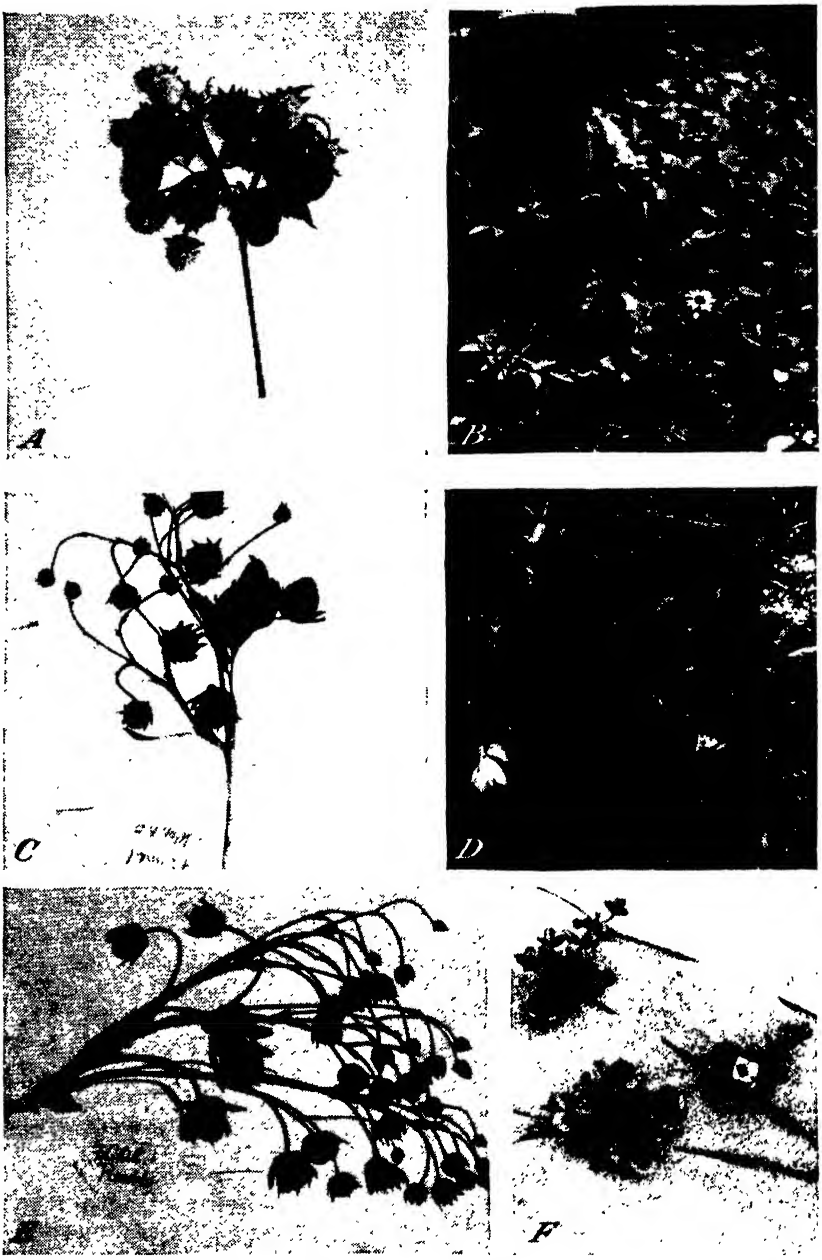

Figure 17.—Native American strawberry species: *A*, *B*, *Fragaria virginiana*, of eastern North America; *C*, *D*, *F. cuneifolia*, of western North America; *E*, *F*, *F. chiloensis*, of the beaches from Alaska to California and of Chile. These are the three 56-chromosome species, from two of which the cultivated strawberry has descended.

Figure 18.—European and Asiatic strawberry species: *A*, *B*, *Fragaria nilgerrensis*, a 14-chromosome strawberry of southern Asia; *C*, *D*, *F. vesca*, the 14-chromosome wood strawberry of Europe; *E*, *F*, *F. moschata*, the 42-chromosome open wood strawberry of Europe. *F. nilgerrensis* is a rather tasteless strawberry but may possibly be of use for breeding. From an everbearing form of *F. vesca* have originated the small alpine strawberries grown in the gardens of Europe. From *F. moschata* have come the high-flavored, rather small Hautbois varieties of Europe.

F. vesca). Yarnell also raised 14-chromosome seedlings from *F. bracteata* × *vesca* var. *rosea*, and Fedorova (*27*) 14-chromosome seedlings from *F. vesca* × *moschata*.

In a similar manner East (*26*) was able to get pairing of one set of chromosomes from *F. vesca* ($n=7$) with a set from *F. virginiana* ($n=28$). Though the resulting diploid seedlings were not as fertile as seedlings of *F. vesca*, the chromosomes were actually related closely enough to pair. Apparently through the ages since the 28-chromosome species originated, some changes have occurred in the chromosomes, but not enough to prevent pairing.

Species With 21 Pairs of Chromosomes

The only known species with 21 pairs of chromosomes is *Fragaria moschata*, which has been discussed above.

Species With 28 Pairs of Chromosomes

Fragaria virginiana, *F. cuneifolia*, and *F. chiloensis*, the group from which the cultivated strawberry has descended, each has 28 pairs of chromosomes. *F. cuneifolia* is the Rocky Mountain wild strawberry, native from Arizona to Alaska and Colorado to Oregon. It has been used very little in breeding. However, its resistance to low winter temperatures and drought and its everbearing character at low elevations indicate its potential value.

Many attempts have been made to cross *Fragaria vesca* and *moschata* with the cultivated strawberry. Such crosses have actually been made, but in carefully controlled tests the seedlings have been entirely or nearly sterile. However, evidence indicates that all four sets of chromosomes of the cultivated strawberry and of the species with 28 pairs of chromosomes had a common origin and are probably homologs of those of *F. vesca*. It seems entirely possible that in some cases where cultivated varieties have been crossed with varieties of *F. vesca*, true hybrid seedlings may have originated by a substitution of 7 chromosomes of *F. vesca* for a set of 7 of the mother plant, and, by a subsequent doubling of the 28, a seedling with the full 28 pairs developed. If the sets are homologs, as suggested by Longley (*41*) and East (*25*) and if those of *F. vesca* should pair with those of the cultivated strawberry, the differences in seedlings might be so slight as to be unnoticed. The everbearing crosses (Chesapeake × *F. vesca* and Early Jersey Giant × *F. vesca*) reported by Van Fleet may have had such an origin, for neither Chesapeake nor Early Giant seedlings would be expected to be everbearing.

Chromosomes of the Strawberry

Yarnell (*63*) studied the chromosomes of strawberries in an attempt to find constant differences among them and concluded that the only constant difference was in length. He found that their small size, their shape, and their position made even an estimate of length difficult. He found the chromosomes of different species very similar. The length averaged 1.7, 1.5, 1.4, 1.3, 1.2, 1.0, and 0.9 microns. The two shorter and the longest were usually easy to distinguish, but the others were not.

Longley (*41*), Yarnell, and Lilienfeld (*40*) all suggest that the chromosome sets in the species with 21 pairs and 28 pairs of chromosomes are homologs. Longley notes also that variability is associated with polyploidy and that the species with 7 pairs of chromosomes are much less variable than the species with 21 or 28 pairs of chromosomes. The diploid *Fragaria* are perfect-flowered, and sex differentiation occurs only in polyploid forms. So far as the wild forms are known, the species with 21 pairs and those with 28 pairs of chromosomes are far more variable than the forms with 7 pairs of chromosomes, and it is evident that variability has come in with polyploidy.

Hybrids Between Chromosome Groups

Millardet (*45*) in France, Richardson (*48, 49, 50, 51*) in England, Solms-Laubach (*56*) in Austria, and Schiemann (*54*) in Germany have made crosses between species of the different chromosome groups. However, the crosses made at the Bussey Institute by East and by two of his students, Mangelsdorf (*43, 44*) and Yarnell (*62, 63, 64, 65*), and reported by these investigators and by Ichijima (*33, 34*), cover most of the species crossed. An outline of the crosses reported by them follows:

Hybrids within the groups having 7 and 28 pairs of chromosomes [8]

Species with 7 pairs of chromosomes:

- *Fragaria californica* Cham. and Schlecht. × *bracteata* Heller (= *californica*), F_1 fully fertile.
- *F. californica* Cham. and Schlecht. × *vesca rosea* Rostr., F_1 fully fertile.
- *F. collina* Ehrh. (= *viridis*) × *maxima* (?), F_1 flowered.
- *F. collina* Ehrh. × *nilgerrensis* Schlecht., F_1 vigorous.
- *F. mexicana* Schlecht. (= *vesca*) × *americana alba* Clute (= *vesca alba* or *vesca americana alba*), F_1 fully fertile.
- *F. americana alba* Clute × *mexicana* Schlecht., F_1 fully fertile.
- *F. vesca rosea* Rostr. × *americana alba* Porter, F_1 fully fertile.
- *F. vesca rosea* Rostr. × *mexicana* Schlecht., F_1 fully fertile.
- *F. vesca rosea* Rostr. × *collina* Ehrh., F_1 partially fertile.
- *F. vesca* L. × *vesca rosea* Rostr., F_1 fully fertile.
- *F. vesca* L. × *nilgerrensis* Schlecht., F_1 dwarfs, no flowers.
- *F. vesca* L. × *americana alba* Porter, F_1 fully fertile.
- *F. vesca* L. × *maxima* (?) (= *vesca* or *vesca maxima*), F_1 partially fertile.
- *F. vesca* L. (Tiflis, Union of Soviet Socialist Republics) × *vesca rosea* Rostr., F_1 fully fertile.
- *F. bracteata* Heller × *vesca rosea* Rostr., F_1 flowered.
- *F. bracteata* Heller × *americana alba* Porter, F_1 fully fertile.
- *F. bracteata* Heller × *collina* Ehrh., F_1 partially fertile.
- *F. bracteata* Heller × *maxima* (?), F_1 partially fertile.
- *F. bracteata* Heller × *nilgerrensis* Schlecht., F_1 dwarfs, no flowers.

Species with 28 pairs of chromosomes:

- *F. chiloensis* Duch. × *virginiana* Duch., F_1 fully fertile.
- *F. virginiana* Duch. × *chiloensis* Duch., F_1 fully fertile.
- *F. virginiana* Duch. × *glauca* Rydb. (= *cuneifolia*), F_1 fully fertile.
- *F. chiloensis* Duch. × *platypetala* Rydb. (= *cuneifolia*), F_1 fully fertile.

Mangelsdorf and East reported on hybrids between different chromosome groups—14 × 42, 14 × 56, 56 × 42—and on generic crosses. *Fragaria vesca* ($2n=14$) × *elatior* (=*moschata*) ($2n=42$) resulted in no F_1 plant that fruited out of 600 seeds. *F. vesca* ($2n=14$) × *chiloensis* ($2n=56$) resulted in 6 nonblooming seedlings out of over

[8]The species names are those given by various authors, followed in some cases by identifications.

1,200 seeds. *F. americana alba* (=*F. vesca alba* or *F. vesca americana alba*) ($2n=14$) $\times$ *glauca* (=*F. cuneifolia*) ($2n=56$) gave only 1 plant from 66 seeds, and it did not bloom. *F. vesca* ($2n=14$) $\times$ *glauca* ($2n=56$) gave 5 nonfruiting plants out of 250 seeds. *F. vesca rosea* ($2n=14$) $\times$ *glauca* ($2n=56$) gave 7 nonfruiting plants from 76 seeds. *F. vesca* ($2n=14$) $\times$ *virginiana* ($2n=56$) gave 21 F_1 plants from 500 seeds, none of which was fertile. *F. bracteata* (=*F. californica*) ($2n=14$) $\times$ *virginiana* ($2n=56$) resulted in 10 nonfruiting plants from 24 seeds and 2 pistillate plants that crossed with *F. vesca rosea.*

F. virginiana ($2n=56$) $\times$ *elatior* ($2n=42$) resulted in 90 plants from 100 seeds, many of the plants being vigorous; all those considered hybrids were sterile.

Yarnell crossed chromosome groups as follows: 14×28, 14×42, 14×56, 42×28, 56×28, and 56×42. The 14×28, 14×42, and 42×28 proved to be nearly or completely sterile. The 56×28 cross gave flowering plants, but none produced pink flowers as would be expected with pink dominant. This is explained by assuming that the crosses were hexaploid $\frac{28 \times 14}{2}$ and that there were four recessive factors for color (*pppp*) and only two dominant factors (*PP*). In a seedling having the composition *PPpppp*, the two dominant genes would be unable to function.

Inheritance in the Species With Seven Pairs of Chromosomes

Richardson (*48*) in England obtained normal hybrid segregation in the species *Fragaria vesca*, with seven pairs of chromosomes. He crossed a trifoliate with a monofoliate plant. The F_1 plants were all trifoliate. When these were selfed he got 177 trifoliate to 73 monofoliate instead of the expected 187.5 to 62.5. He also crossed a white- with a red-fruited variety. The F_1 plants were red-fruited but when selfed gave 70 red-fruited to 20 white, which is close to the theoretical 67.5 to 22.5. In crosses between single- and double-flowered forms the F_1 was single but gave 155 single to 62 double in the F_2 instead of 163 single to 54 double. A cross between runnerless and runner-producing gave runner-producing in the F_1, but 342 runner-producing to 97 runnerless in the F_2 instead of the expected 329 runnered to 110 runnerless. Though the above four characters showed inheritance not far different from the expected 3 to 1 ratio, Richardson had difficulty in classifying his F_2 in a cross between pink- and white-flowered plants. Mangelsdorf and East, however, obtained 128 pink and 46 white in a similar cross, which is very close to the expected 3 to 1 ratio. They also crossed red- with white-fruited plants and obtained 102 red-fruited to 56 white-fruited plants instead of 118.5 red to 39.5 white.

Generic Crosses

Fragaria vesca ($n=7$) $\times$ *Duchesnea indica* (L.) Focke ($n=42$) resulted in 30 plants from 500 seeds, 26 being hybrids, all small and weak. *F. vesca* ($n=7$) $\times$ *Potentilla nepalensis* Hook. (n unknown) resulted in 2 seedlings from 141 seeds, but both died before flowering. Crosses between the strawberry and the raspberry have been reported, but the proof of such crosses has not been fully established. The so-called strawberry-raspberry is not a hybrid but a low-growing

raspberry from China; and the so-called tree strawberry is simply a species of tree, *Arbutus unedo* L., bearing fruit with a slight resemblance to a strawberry.

Unusual Inheritance in Fragaria

Paternal inheritance.—Millardet (*23, 24, 45*) reported four cases in which the seedlings resembled the male parent. These crosses were *Fragaria vesca* × Globe, *F. vesca* × Ananas, *F. vesca* × *chiloensis* ($n=7 \times n=28$ crosses), and *F. moschata* (*elatior*) × Globe ($n=21 \times n=28$). Though the first two crosses gave sterile seedlings and the last two gave seedlings with reduced fertility, they may have been physiological males or imperfect hermaphrodites. Ichijima (*33*), working at East's laboratory, counted chromosomes of several patroclinous hybrids and found them equal to the sum of the haploid numbers of the parents. In a cross of *F. vesca* (*rosea* × *alba*) × *virginiana*, however, Ichijima found one plant with a somatic number of 56 chromosomes that was close to *F. virginiana* in appearance. Yarnell has also reported two octoploid seedlings from crosses of $n=7 \times n=28$ plants. Longley also reported a cross of *F. vesca alba* × Aroma where the seedling resembled the male parent and had the same chromosome number. Rygg and Darrow (*53*) found a considerable percentage (1.2 percent) of such plants out of 3,519 crosses of cultivated varieties × *F. cuneifolia*, both with parents with 28 pairs of chromosomes. Waldo has also found 5 plants of the maternal, 22 of the paternal, and 6 of the hybrid types in a cross of *F. chiloensis* × *cuneifolia*. The full explanation of this appearance of seedlings identical with or very like the male is not yet apparent. However, an observation of Ichijima that the pollen mother cells have two nuclei, and observations by Rudloff (*52*) that two complete embryo sacs were often seen side by side in *F. virginiana* and *F. vesca* and that they may fuse, may have some bearing on this.

Pairing of chromosomes in an artificial polyploid.—When fertile tetraploids originated as the result of a cross of *Fragaria bracteata* (= *F. vesca californica*) × *vesca rosea*, Yarnell (*64*) concluded that the four homologous chromosomes paired at random. That is, the sets of seven chromosomes in each species were sufficiently alike so that the long chromosomes from *F. bracteata* might pair with the long ones from *F. vesca rosea*, and the short with short. However, a critical review of the *vesca* group indicates that *bracteata* might better be classed as a botanical variety, *F. vesca californica*, coordinate with *rosea*. If this classification be made, the chromosomes of this hybrid may be considered homologs of these botanical varieties of *vesca*.

Again in a cross of *Fragaria vesca alba* ($n=7$) × *virginiana* ($n=28$), East obtained a diploid hybrid. Nine of the F_2 were fertile, three seedlings did not flower for the 3 years they were observed, and seven were sterile. It is noteworthy that a set of seven chromosomes of *F. virginiana* paired with a set of *F. vesca alba* well enough to form some fertile seedlings. Yarnell also reported diploid hybrids of *F. vesca rosea* ($n=7$) × *glauca* (= *F. cuneifolia*) ($n=28$) and of *F. vesca alba* ($n=7$) × *chiloensis* ($n=28$).

Pairing of nonhomologous chromosomes.—Yarnell (*64*) reported that tetraploid plants resulting from crosses of *F. bracteata* × *vesca rosea* were

crossed with three species having seven chromosomes. The seedlings were triploids with 21 somatic chromosomes. Examination showed that the nonhomologous chromosomes paired. Later he reported other similar instances. Conditions were present—possibly high temperatures—that made possible the pairing of chromosomes that were not homologs, even though pairing of homologous chromosomes only is supposed to be essential to the Mendelian conception of heredity.

Production of homozygotes through induced parthenogenesis.—A single-factor pair, *Pp*, was found by East (*24*) and his students to be responsible for pink and white color of flower, and another pair, *Rr*, for red and white fruit color in the diploid species. In crossing *F. bracteata* × *vesca rosea*, a heterozygous red-fruited, pink-flowered plant was obtained. Among the diploid plants produced by crossing (*F. bracteata* × *vesca rosea*) × *virginiana* and × *chiloensis* there were 12 with red fruit and pink flowers, 3 with white fruit and pink flowers, 7 with red fruit and white flowers, and 2 with white fruit and white flowers. Some, or more probably all, of these diploids were considered to have arisen through induced parthenogenesis, that is, the embryo must have developed without fertilization. At the beginning of development, then, the organism was a haploid, but because the seedlings all proved to be diploids, the haploid chromosomes must have divided. Thus, the seedlings were homozygotes. East (*25*) points out that if a means can be found for inducing parthogenesis from which homozygous diploids develop, it might eliminate the uncertain and costly methods now employed to obtain plants that are homozygous.

Bud Selection in the Strawberry

Bud selection in the strawberry has never been a method of obtaining improved varieties or strains, as in apples, oranges, etc. Only a few kinds of bud sports have been observed. Only the probable production of an everbearing sport in the case of the Pan-American and of a noneverbearing sport in the case of the June Rockhill have had economic value. Another kind of sport—variegated foliage—is a serious limitation to the value of such varieties as the Blakemore, Howard 17, and many others.[9] Bud sports of many plants result in the appearance in somatic tissue of recessive characters. Thus, in the strawberry, selfed seedlings of varieties that sport to variegated plants show a proportion of yellow seedlings. If, as the evidence given above indicates is probable, most characteristics are quantitative, then a change in a single gene in one of the eight chromosomes is not likely to make enough of a change in the external appearance of the plant to be noted or measured.

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APPENDIX

TABLE 1.—*Past and present workers at experiment stations who have devoted or are devoting part or all of their time to strawberry improvement*

Location	Early workers	Present workers
UNITED STATES		
Federal stations:		
Glenn Dale and Beltsville, Md.	W. Van Fleet, George F. Waldo	George M. Darrow.
Corvallis, Oreg.	R. H. Roberts, V. R. Gardner, C. E. Schuster, B. S. Pickett, G. L. Rygg, George M. Darrow.	George F. Waldo.
Cheyenne, Wyo.		LeRoy Powers, A. V. Hildreth.
State stations:		
Alaska, Sitka	C. C. Georgeson	
California, San Jose and Davis	William T. Horne, A. G. Plakidas.	E. V. Goldsmith, H. E. Thomas.
Colorado	C. S. Crandall	
Connecticut, New Haven		D. F. Jones, W. R. Singleton.
Florida, Plant City	A. N. Brooks	
Georgia, Experiment	J. G. Woodruff	H. P. Stuckey, H. L. Cochran, J. E. Bailey.
Hawaii, Honolulu		A. G. Mangelsdorf.
Illinois, Urbana	J. E. Vaile	A. S. Colby.
Iowa, Ames	J. L. Budd, G. A. Ivins	
Louisiana, Baton Rouge		J. C. Miller, W. D. Kimbrough, A. G. Plakidas.
Maine, Orono		R. M. Bailey.
Massachusetts, Amherst		A. P. French.
Minnesota, Excelsior	Charles Haralson, M. J. Dorsey, W. D. Valleau.	A. N. Wilcox, W. H. Alderman, E. Angelo, W. G. Brierley. F. E. Haralson.
Missouri:		
Columbia	J. W. Clark, C. A. Keffer	
Mountain Grove		Paul H. Shepard, Guy Rook.
Nebraska, Lincoln	R. F. Howard, C. C. Wiggins	
New Hampshire, Durham	B. S. Pickett	
New Jersey, New Brunswick		J. H. Clark.
New York, Geneva	C. J. Hunn, S. A. Beach, W. Paddock, R. D. Anthony, O. M. Taylor.	George L. Slate, R. Wellington.
North Carolina, Raleigh	W. F. Massey	
North Dakota, Fargo		A. F. Yeager, D. H. Scott.
Ohio, Wooster	Paul Thayer	
Rhode Island, Kingston	F. W. Card, G. E. Adams	
South Dakota, Brookings	Charles Haralson	N. E. Hansen.
Tennessee, Knoxville	J. A. McClintock, E. M. Henry	B. S. Drain, C. D. Sherbakoff.
Texas, Winter Haven		E. Mortensen, S. H. Yarnell.
Vermont, Burlington	M. B. Cummings, E. W. Jenkins.	
Washington, Puyallup	M. B. Hardy	C. D. Schwartze.
Wisconsin, Madison		R. H. Roberts.
FOREIGN		
Canada:		
Dominion Experimental Farm, Ottawa.	W. T. Macoun, A. J. Logsdail.	M. B. Davis.
Nova Scotia, Kentville		W. S. Blair.
Alberta, Lacombe	F. H. Reed	F. H. Reed.
British Columbia, Sidney	F. E. Buck	E. M. Straight.
Manitoba, Morden		W. R. Leslie.
Ontario:		
Vineland	F. S. Reeves	W. S. Strong, E. F. Palmer.
Guelph	D. A. Kimball	
England:		
Long Ashton, Bristol	C. W. Richardson	J. G. Maynard, G. T. Spinks.
East Malling, Kent		W. S. Rogers.
John Innes Horticultural Institution, Merton.		
Norway, Njos, Hermansverk		P. Stedje.
Sweden, Alnarp		C. G. Dahl.
Germany:		
Berlin, Institute for Tree Fruits of the University.		Prof. Kemmer.
Muncheberg, Kaiser Wilhelm Institute for Genetics.		Dr. Rudorf.
Pillnitz, Research Station for Garden Plants.		Prof. Schindler.
Switzerland, Geneva		F. Chodat.
Czechoslovakia, Pruhonice		Landovsky.
Union of Soviet Socialist Republics:		
Trudy		N. Ia. Federova.
Mitchurin Institute		A. Petrov, V. G. Lithovitser.
Japan	H. Kihara, K. Ichijima	F. A. Lilienfeld.
Australia: New South Wales, Sydney.		H. Wenholz.

TABLE 2. *Strawberry varieties originated by public agencies*

Location	Variety	Year introduced	Parentage	Superior qualities	Estimated acreage
UNITED STATES					
Federal station					
Beltsville, Md ...	Blakemore	1929	Missionary × Howard 17	Firm light red preserving southern	16 000
	Bellmar	1931	do	Attractive good flavor large	200
	Southland	1931	Ettersburg 80 × Howard 17	Attractive, high flavor in south, disease resistant	50
	Redheart	1931	Portia × Fairfax	Very firm canning resistant to crinkle	700
	Dorsett	1932	Howard 17 × Royal Sovereign	Vigor, high flavor, disease-resistant	4,000
	Narcissa	1932	do	do	100
	Fairfax	1932	Unknown	do	500
	Oxheart	1933	do	Firm, deep red, high flavor	None
State stations					
Alaska, Sitka	President Harding		Hollis × *Fragaria chiloensis*	Productive in Alaska firm high flavor	
Minnesota, Excelsior	Duluth	1923	Pan American × Dunlap	Productive, everbearer, hardy	Small
	Minnesota	1920	Dunlap × Pocomoke	Productive, attractive high flavor	Do
	Minnehaha	1920	Minnesota × Abington	Vigorous, hardy, large firm, late	Do
	Chaska	1922	(Dunlap × Pocomoke) × Brandywine	Attractive, high quality	Do.
	Easypicker	1922	Dunlap × unknown	do	Do
	Nokomis	1922	Dunlap × Abington	Productive, large	Do
	Deephaven	1922	Unknown	Everbearer	Do
New Jersey, New Brunswick	N. J. 35	1930		Attractive, productive	20
New York, Geneva	Hunn	1895	Johnson Late × Sharple	Late attractive	None
	Prolific	1908	Sample × Marshall	Very productive attractive	Do
	Magnus	1910	Hunn × Marshall	High flavor, large	Do
	Quality	1910	Hunn × Atlantic	High flavor, late	Do
	Addison	1918	President × Marshall	Productive, mild, large	Do
	Alden	1918	do	Productive, glossy, large	Do
	Angola	1918	do	do	Do
	Arcade	1918	do	Productive, firm, large	Do
	Argyle	1918	do	Productive glossy large	Do
	Ashton	1918	do	do	Do
	Athens	1918	do	Productive bright red large	Do
	Aurora	1918	Seedling of Prolific	Vigorous firm, large	Do
	Beacon	1923	President × Marshall	Early, large attractive	Small
	Bliss	1923	Chesapeake × Atkins	Late high flavor, attractive	Do
	Boquet	1923	Chesapeake × Pan American	Firm productive	Few acres
	Caledonia	1929	Marshall × Howard 17	Preserving	Small
	Camden	1931	do	Mild, productive, vigorous	Do
	Cato	1929	do	Vigor, high flavor	10
	Catskill	1933	do	Very large attractive productive	500
	Clermont	1929	do	Attractive holds up in size	100
	Culver	1931	do	Preserving, attractive	Small

TABLE 2.—*Strawberry varieties originated by public agencies*—Continued

Location	Variety	Year introduced	Parentage	Superior qualities	Estimated acreage
UNITED STATES—continued					
State stations—Continued.					
North Dakota, Fargo	Dry Weather	1925	Americus × Howard 17	Sweet, drought-resistant, everbearer	2.
Oregon, Corvallis	Corvallis	1930	Ettersburg 121 × Marshall	High flavor, fine texture, canner, freezing	150.
South Dakota, Brookings (51).	Dakota No. 1	1907	Jessie × Manitoba Wild	Possibly hardiest variety	Small.
	Dakota No. 2	1907	Glen Mary × Cavalier Wild	Hardy	None.
Tennessee, Knoxville	McClintock	1932	Aroma selfed	Large, productive	Small.
FOREIGN:					
Canada:					
Dominion Experimental Farm, Ottawa.	Bianca	1913			None.
	Cassandra	1913	Seedling of Bubach	Large, glossy, late, attractive	Some.
	Celia	1913			None.
	Cordelia	1913	Seedling of Bubach	Deep salmon color, productive	
	Desdemona	1913	do	Dark red, good flavor	Do.
	Francesca	1913			Do.
	Helana	1913			Do.
	Hermia	1913	Seedling of Wm. Belt	Firm, attractive	Do.
	Julia	1913	Seedling of Bubach		Do.
	Lavinia	1913			Do.
	Lucetta	1913	Seedling of Bubach	Firm, attractive	Do.
	Mariana	1913	do	Productive, attractive	Do.
	Miranda	1913		Large, glossy	Do.
	Octavia	1913			Do.
	Olivia	1913			Do.
	Ophelia	1913	Seedling of Wm. Belt	Large, bright scarlet	Do.
	Portia	1913	do	Firm, excellent canner	Some.
	Viola	1913	Seedling of Wm. Belt	Firm, large	Do.
	Virgilia	1913	do	Deep red, large	Do.
Alberta, Lacombe	Lacombe	1928	Late Stevens × Dunlap	Hardy, good preserver	
British Columbia, Sidney	New Victoria	1930	Royal Sovereign × Magoon	Large, firm, drought-resistant	
Ontario:					
Guelph	O. A. C	1925	Parsons × Howard 17	Large, glossy, red	
Vineland	Valentine	1919	Williams × Brandywine	Excellent flavor	None.
	Valet	1919	do	Large, similar to Joe	Do.
	Valiant	1919	Brandywine × Williams	Oval, smooth	Do.
	Valid	1919	Dunlap × Ozark	Large, dark, productive	Do.
	Valonic	1919	do	Light, bright color	Do.
	Valor	1919	do	Early	Do.
	Vambrace	1919	do		Do.

	Van Dyke	1919	do.	Early, productive	Some.
	Vanessa	1919	Dunlap × Brandywine	Large, home use	None.
	Vanguard	1919	Pocomoke × Ozark		Do.
	Vanilla	1919	Dunlap × Williams	Large, attractive	Do.
	Vanquish	1919	Dunlap × Pocomoke	Late	Do.
	Vantage	1919	Williams × Ozark	Large, firm, dark	Do.
	Vaquero	1919	Williams × Dunlap	Large	Do.
	Varangian	1919	do	Large, firm	Do.
	Vassal	1919	Ozark × Williams	Early	Do.
	Vast	1919	Ozark × Michel	do	Do.
	Vaunt	1919	Brandywine × Michel	do	Do.
	Vavasor	1919	Pocomoke × Ozark	Large	Do.
	Vaward	1919	do	Early	Do.
	Vector	1919	do	Large, bright	Do.
	Veda	1919	Sample × Dunlap	Very large	Do.
	Vena	1919	Parsons × Michel	White flesh	Do.
	Vendance	1919	Nettie × Williams	Very late, large	Do.
	Vendor	1919	Dunlap × Ozark	Large, very dark	Do.
	Vendue	1919	Williams × Ozark	High flavor, early	Do.
	Venus	1919	Joe × St. Louis	Large, very late	Do.
Manitoba, Morden	Rosthern	1929		Hardy, large, light color	Do.
Czechoslovakia, Pruhonice	Prof. Jelinck		M. Moutot × Deutsch Evern	Early, hardy	
	Bonmir Landovsky		Kentish Favorite × Deutsch Evern	Early, firm, large	
England:					
Merton, John Innes Horticultural Institution.	Richardsons Seedling			Sweet	
	Seedling D_1			do	
Germany, Pillnitz	Oberschlesien [1]	1924		Large, deep red, vigorous, productive	
	Johannes Muller				
	Frau M. Schindler				
	Pillnitz				
	Herbstfreude				
	Mathilde				
Sweden, Alnarp	Inga	1933	Frau Direktor Echtenmeyer × V. H. de Thury.	Early, excellent flavor	
	Stella	1933	do	do	
	Luna	1934	Late Leopold × V. H. de Thury	Early, excellent flavor, productive	

[1] Raised by Max Richter.

TABLE 3.—*Strawberry varieties originated by private breeders*

Name and address	Variety	Year introduced	Parentage	Superior qualities	Estimated acreage
C. H. Beaver, Eau Claire, Wis.	Beaver	1925	Howard 17 × Burrill	Hardy, productive, good shipper	2,000.
E. C. Howard, and father, A. B. Howard, Belchertown, Mass.	Dighton	1908		High flavor	
	Howard 17	1909	Crescent × Howard No. 1	Early, productive, large, attractive, frost and disease resistant.	32,000.
	Howard Supreme	1929	Howard 103 × Howard 17	Productive, high flavor, excellent for freezing	75.
J. E. Kuhns, Cliffwood, N. J.	Aberdeen	1923		Productive, resistant to brown stele disease	2,000.
George Voer, Peru, Ind.	Mastodon	1924	Kellogg Prize × Superb	Productive, everbearing, produces runners freely	1,000.
Keith Bros., Sawyer, Mich.	Kanner King	1932		Dark red, firm, canner	Small.
	Joan	1933	Ananas de Guemene × Mastodon	Large, everbearing	
	Uncle Cap	1933	Mastodon seedling	Large, sweet, everbearing	
H. Rockhill, Conrad, Iowa	Francis	1910	Louis Gautier × Pan American	Very good flavor, everbearing, early	None.
	Americus	1911	do	Excellent flavor, everbearing	Do.
	Iowa	1911	Dunlap × Pan American	Everbearing	Do.
	Progressive	1911	Pan American × Dunlap	Everbearing, vigorous, very hardy, excellent flavor, early, healthy.	200.
	Standpat	1914	do	Everbearing, large	None.
	Rockhill (Wazata)	1922	Progressive × Early Jersey Giant	Everbearing, large, one of best flavored berries in United States, large, disease-resistant, very hardy.	200.
	June Rockhill	1932	Rockhill sport	Noneverbearing, but like Rockhill otherwise	Small.
Gardner Nurseries, Osage, Iowa	Red Gold	1925	Howard 17 × Everbearer	Sweet, large	
	Gardner 1000	1918		Everbearing, propagates freely	
	Gardner 999	1925		Everbearing, high flavor	
W. Kosuga, Sandy, Utah	Berri Supreme	1929		Everbearing	20.
	Twentieth Century	1936	Berri Supreme × Rockhill	do	
A. F. Etter, Ettersburg, Calif.	Rose Ettersburg	1903	(Sharpless × Parry) F_2 × *Fragaria chiloensis*, Peru.	Vigorous, productive, fragrant, drought-resistant	None.
	Ettersburg 121	1907	Derived from *F. chiloensis* × ?	Vigorous, many crowns, hardy foliage, best canner in United States, solid, high flavor, very late.	250.
	Ettersburg 80	1912	In part at least from Rose Ettersburg and a selection of *F. chiloensis*	Vigorous, large, healthy foliage, solid flesh, large	Little in the United States, but some in Australasia.
	Nor-J	1913	Fendall × Ettersburg 121	Productive, firm	None.
	Ettersburg 76	1913	(Michel[1] × Rose Ettersburg) × *F. chiloensis*.		Do.
	Ettersburg 84	1913	Sister to Ettersburg 80.	Vigorous	Do.
	Ettersburg 86			Firm, pale	Do.
	Ettersburg 89	1913	Dornan and *F. chiloensis*	Vigorous, few runners	Do.
	Ettersburg 111	1913	Sister to Ettersburg 80	Productive, drought-resistant	Do.
	Ettersburg 112	1913	do	Large, glossy	Do.

Ettersburg 91	1914	do	Deep red, high flavor, drought-resistant	Do
Ettersburg 71	1914		Cap or calyx stays on plant, light pink	Do
Ettersburg 75	1914	(Michel [1] × Rose Ettersburg) × *F chiloensis*	Red to center, firm	Do.
Ettersburg 79	1914	do	Deep red, high flavor	Do
Ettersburg 88	1911	Wm Belt cross	Deep red, canning variety	Do
Ettersburg 93	1914	Sister to Ettersburg 80	Deep, glossy red	Do
Ettersburg 94	1914	Rose Ettersburg × *F chiloensis*	Very attractive, acid	Do
Ettersburg 106	1914	do	Vigorous, pink, evergreen	Do
Ettersburg 114	1914	Rose Ettersburg × Michel [1] × –	Similar to Ettersburg 94	Do
Ettersburg 116	1914	Sister of Ettersburg 91	do	Do
Ettersburg 200	1914	Dunlap × *F chiloensis*, Peru	Pink, productive, deep-set seeds	Do
Ettersburg 330		Ettersburg 24 (Michel × Rose Ettersburg) cross	--	Do.
Ettersburg 450	1920	- ---	Excellent flavor, large, firm, attractive	Do
Ettersburg 904			Sweet, very firm	Do
Euresko (Eurisko)	1916	Chesapeake × Ettersburg 20 (Rose Ettersburg × *F chiloensis*)	Deep red to center, firm	Do
Beaderarena	1916	*F chiloensis* × Bederwood	Very hardy foliage, attractive	Do
Califour	1918	Ettersburg 88 × 2	Deep red, black raspberry flavor	Do
Delecto	1918		Juicy, high flavor, late	Do
Fendalemo	1918		Deep red, vigorous	Do
Beaderarena, Jr		Seedling of Beaderarena	High flavor, sweet .	Do
Fantastic	1918	Fendall × Ettersburg 121	Vigorous large	Do
Ossie	1918	Seedling of Ettersburg 81	Meaty flesh, early, showy	Do
Cream	1920	Ettersburg 330 × Trebla	Yellow cream color, productive, late	Do
Fendalcino	1920	Fendall × Ettersburg 121	Large, resistant to heat, productive	Do
Kalicene	1920	Ettersburg 216 × Trebla or Ettersburg 121 × Trebla	Early, solid flesh, very productive red center, vigorous	Do
Lnge	1920	Unknown	Canning, solid, brilliant red, firm	Do
Red Cross	1920	Ettersburg 216 × Trebla	Very glossy, sweet, attractive, uniform shape	Do
Rena	1920	Probably *F chiloensis* × Ettersburg 84	Light pink, similar to *F chiloensis*, late	Do
Trebla	1916	Ettersburg 114 × Ettersburg 84	Firm, solid, productive, frost resistant	Small
White Sugar	1920	Unknown	White to pink, sweet, firm, large, late	None
Red Sugar		Cross of Ettersburg 80		Do
Late Cross		Seedling of Red Cross	Late, resembles Ettersburg 80	Do
Redfour		Ettersburg 121 × Trebla	Large, canner, early	Do
Von Humboldt	1930	(Rose Ettersburg × *F chiloensis*) × cross of similar parentage	Evergreen, heavy foliage, vigorous	
Alcatraz		Red Sugar × Kalicene	Meaty	
Wickson	1930	(Red Sugar × Ettersburg 121) × *F cuneifolia*	Evergreen, heavy foliage, firm	
Golden Gate		Red Sugar × Kalicene	Firm, high flavor, large	
Elinor	1933		Pink	
Hard	1933		Firm, meaty	
Kandykid			Deep red, firm canning	
New Deal	1935	Probably Red Sugar × Ettersburg 121 or Trebla		--
Gracilis	1935	*F chiloensis* hybrid	. .	--

[1] Not true Michel, as Mr Etter reports it as pistillate while Michel is perfect flowered

TABLE 3.—*Strawberry varieties originated by private breeders*—Continued

Name and address	Variety	Year introduced	Parentage	Superior qualities	Estimated acreage
Thomas Laxton, Bedford, England.	Traveller	1872	La Constante × Napier	Deep scarlet	
	Exquisite	1874			
	Pioneer	1876		Large, attractive	
	Noble	1884	Seedling of Sharpless	Large, attractive, productive, wide adaptation	
	Captain	1884	Crown Prince × Foreman Excelsior	Most attractive of all, early	
	A. F. Barron	1885	Sir J. Paxton × Sir C. Napier	Glossy, scarlet	
	Jubilee	1887		Late	
	King of the Earlies	1888	Vicomtesse × Black Prince	Very early, high flavor	
	Commander	1889	British Queen × President	High flavor	
	Competitor	1890	Kerr Prolific × Foreman Excelsior		
	Scarlet Queen	1891	King of the Earlies × Noble	Early, attractive, high flavor	
	White Knight	1891	King of the Earlies × Noble	Light scarlet × white	
	Royal Sovereign	1892	Noble × King of the Earlies	Large, bright, scarlet, firm, high flavor	
	Latest of All	1894	British Queen × Helena Gloede	Late, very large, crimson, productive	
	Monarch	1895	Latest of All × Captain	Large, attractive	
	Leader	1895	Latest of All × Noble	Large, deep crimson, sweet	
	Laxton No. 1		Noble × May Queen	Earliest	
	Bedford Champion	1895	Seedling (Scarlet Queen × John Ruskin) × seedling (Noble × Sir J. Paxton.)	Very large, scarlet, sweet	
	Mentmore	1897	Noble × British Queen	Crimson	
	Fillbasket	1897	Royal Sovereign × Latest of All	Scarlet, productive	
	Reward	1898	Royal Sovereign × British Queen	Large, high flavor, attractive	
	Trafalgar	1900	Latest of All × ?	Late, large, attractive	
	Climax	1901	Latest of All × Waterloo	High flavor, large, firm	
	The Laxton	1901	Royal Sovereign × Sir J. Paxton	Large, firm, vigorous	
	The Bedford		Dr. Hogg × Napier	High flavor, scarlet	
	Latest	1904	Latest of All × seedling	Very large, week later than Waterloo	
	Progress	1906	British Queen × Latest of All	Late, bright scarlet, large	
	Cropper	1907	Seedling × Fillbasket	Productive, large, crimson	
	Reliance	1907	V. H. de Thury × seedling of St. Joseph.	Productive, scarlet	
	Perpetual	1907	Monarch × St. Joseph	Large, sweet	
	Profit	1908	Sir J. Paxton × Countess	Firm, productive, deep scarlet	
	Rival	1909	Givons Late × Royal Sovereign	High flavor, late, deep scarlet	
	Utility	1909	Seedling 500 × Waterloo	Firm, high flavor	
	Connoisseur	1909	Scarlet Queen × Fillbasket	Excellent flavor, bright scarlet	
	Epicure	1909	British Queen × Fillbasket	Excellent flavor	
	Pine Apple	1909		Excellent flavor, bright scarlet	
	Unique			Crimson	
	The Count			do	
	Maincrop	1910	Bedford Champion × The Laxton	High flavor, large	
	The Earl	1911	Waterloo × Royal Sovereign	Preserving	

The Admiral	1914	Seedling × Bedford Champion	High flavor, productive, large
White Perpetual	1916	Louis Gauthier × St Antoine	Nearly white, everbearing
Everbearing	1916	-	High flavor
International	1916	Latest of All × seedling	Bright scarlet, firm, high flavor
King George V	1916	Royal Sovereign × Louis Gauthier	Bright scarlet, forcing, early
The Duke	1916	Seedling × Bedford Champion	Early, high flavor, scarlet, forcing
Tit Bit	1918	Reliance × Bedford Champion	High flavor, scarlet
Victory	1919	Seedling × British Queen	Crimson, sweet
Sir Douglas Haig	1919	Seedling × Dr Hogg	Scarlet, yellow seeds, sweet
Marshal Foch	1920	The Bedford × Sir Joseph Paxton	Firm, dark
Lord Beatty	1920	Seedling × Bedford Champion	Light red
Laxtonian	1921?	Seedling × seedling	High flavor, glossy, crimson, firm, large
Bountiful	1921	D × D	Scarlet, large
Abundance	1922	Fillbasket × The Earl	High flavor, large, sweet
Omega	1923	Seedling × Bedford Champion	Latest, sweet, scarlet, firm
Majestic	1924	Seedling × International	Bright, crimson, sweet, firm
Rearguard	1925	Latest × Omega	Late, sweet, productive
Robust	1925	Bedford Champion × Bedford	Crimson, sweet
Empress	1925	Seedling × seedling	Firm, preserving
Prolific	1926	do	Scarlet, sweet, resists mildew
Duchess of York	1927	Laxtonian × Duke	Bright scarlet, drought resistant
Primate	1928	Seedling × seedling	Firm, sweet, bright crimson
Acquisition	1929	do	Vigorous, disease resistant
The Queen	1929	Waterloo × Queen of Denmark	High flavor, pale scarlet

Sources of Superior Qualities in Strawberries

Note.—Though the following varieties and species are notable for superior qualities, it may be that they will not prove to be equally good transmitters of these qualities.

Plant characteristics:

Hardy against cold: *Fragaria cuneifolia* selections and crosses (Beltsville, Md., Corvallis, Oreg., Fairbanks, Alaska, and Cheyenne, Wyo.); *F. virginiana* selections (Fargo, N. Dak), Dakota, Dry Weather, Dunlap, Rockhill, Progressive, Parsons (Gibson), Beaver, Camden, Culver, Minnehaha.

Resistant to frost: Howard 17 and Chesapeake in United States, Sir Joseph Paxton in England.

Resistant to verticillium wilt: Chilean (*F. chiloensis*).

Resistant to brown stele (*Phytophthora*): Aberdeen, Mastodon, and Redheart in Illinois; Leopold and Oberschlesien in Scotland.

Resistant to leaf scorch: Southland, Fairfax, Howard 17, Dorsett. U. S. D. A. 1142 (652 × Ettersburg 450), 1572 (Howard 17 × Dorsett), 2124 (Chesapeake × Fairfax).

Resistant to leaf spot: Southland, Fairfax, Howard 17, Rockhill, U. S. D. A. 1142 (652 × Ettersburg 450), U. S. D. A. 2120 (Chesapeake × Fairfax), U. S. D. A. 2124 (Chesapeake × Fairfax).

Resistant to mildew: Marshall and Rockhill in the United States; V. H. de Thury (Stirling Castle), McMahon, and Aberdeen Favorite in England.

Resistant to aphid: Late Leopold, Bedford Champion, Aberdeen Standard, John Ruskin, Marshal Foch, and Sturton Cross in England.

Resistant to mite: Marshall in California; Mme. Kooi, Laxtonian, and Oberschlesien in England.

Resistant to crinkle: Redheart, Rockhill, and some *F. chiloensis* hybrids in Oregon.

Resistant to yellows (xanthosis): Nick Ohmer, Bellmar, and probably some *F. chiloensis* hybrids in California.

Resistant to heat: Missionary, Klondike, Blakemore, Southland, U. S. D. A. 1142 (652 × Ettersburg 450).

Resistant to drought: *F. cuneifolia*, U. S. D. A. 1791 (Ettersburg 904 × Howard 17), Marshall, Gold Dollar; The Duke and Waterloo in England.

Greenhouse forcing: Marshall in the United States; Royal Sovereign in Europe; Deutsch Evern in frames in the Netherlands; Noble in low houses in Germany.

Adapted to short days: Missionary, Klondike, Blakemore in the United States; Chilean in Ecuador.

Fruit characteristics:

Early ripening: U. S. D. A. 2267 (Missionary × Fairfax), U. S. D. A. 1631 (Howard 17 × Dorsett), Michel, Blakemore, Dorsett, Howard 17, Ozark, Progressive, Rockhill, Beaver, Early Bird, Minn. 1200; Deutsch Evern, Avant Tout, Laxton No. 1, and The Duke in England; Sir John Ruskin in Scotland.

Late ripening: U. S. D. A. 2263 (Ettersburg 904 × Fairfax), U. S. D. A. 2124 (Chesapeake × Fairfax), *F. chiloensis* and its crosses (Corvallis, Oreg., and New Brunswick, N. J.), Ettersburg 121, Wyona, Pearl, and Gandy. Omega, Latest, Utility, Jucunda, Rearguard, Givons, Waterloo, and Leopold in England.

Firm: U. S. D. A. 2166 (Joe × Redheart), U. S. D. A. 2120 (Chesapeake × Fairfax), Redheart, Fairfax, Blakemore, Minnehaha, U. S. D. A. 2161 (Joe × Redheart). Many Chesapeake × Fairfax and Blakemore × Fairfax selections have firm fruit.

Large: U. S. D. A. 2132 (652 × Fairfax), N. C. 337 (Bellmar × Fairfax), Catskill, Dorsett, Marshall, Minnehaha, Minn. 1201 (Marshall selfed). Latest and Laxtonian in Europe.

Yellow seeds: Blakemore, Chesapeake, U. S. D. A. 2061 (652 × Ettersburg 450), U. S. D. A. 1591 (Howard 17 × Dorsett), U S D. A. 2126 (Chesapeake × Fairfax).

Light scarlet color: Blakemore in United States; Royal Sovereign, Fillbasket, The Duke, The Queen, King George V in England.

Superior qualities for freezing: Fruitland, Joe, Big Late, Klondike in eastern United States; Howard Supreme in Massachusetts; Corvallis, Redheart (sliced), Marshall in Oregon and Washington. Also, selections from Blakemore × Ettersburg 450, Southland × Blakemore, Blakemore × Marshall, Blakemore × Klon-

dike, Redheart × Ettersburg 121, Blakemore × Ettersburg 121, Ettersburg 121 × Clark, Clark × Narcissa, and Howard 17 × Marshall in Oregon.

Superior qualities for preserving: Blakemore in United States; V. H. de Thury and Deutsch Evern in Europe. Reported good in some localities: Culver and Dorsett in United States; Lacombe in Canada. Marshall and Missionary are extensively used for preserving, though they are not equal to Blakemore. Crosses of Blakemore with other varieties have proved superior for preserving.

Superior qualities for canning: Redheart, Corvallis, Ettersburg 121 in the West; Portia in the East. Reported good in some localities: Culver, Redfour, Lnge, Trebla. Probably Noble, Scarlet Queen, and Paxton in parts of northern Europe. Crosses of Narcissa × Ettersburg 121, Redheart × Ettersburg 121, and Oregon 14 (Ettersburg 121 × Marshall) × Narcissa have produced good canning selections in Oregon.

Excellent flavor: Dorsett, Fairfax, Rockhill, Southland, Marshall, Corvallis, U. S. D. A. 1008 (*F. chiloensis* × Progressive), U. S. D. A. 1128 (Howard 17 × Ettersburg 450), U. S. D. A. 2183 (Missionary × Howard 17). British Queen, Dr. Hogg, Scarlet Queen, Connoisseur, Epicure, Pineapple, The Duke, Aberdeen Standard, and Royal Sovereign in Europe.

Unusual flavors: U. S. D. A. 1021 (Kalicene × Howard 17), grape flavor; U. S. D. A. 1026 and 1028 (Howard 17 × Ettersburg 450), apricot flavor; U. S. D. A. 1145 (652 × Ettersburg 450), raspberry flavor; Califour, black-raspberry flavor.

BLACKBERRY AND RASPBERRY IMPROVEMENT

GEORGE M. DARROW, Senior Pomologist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry [1]

BLACKBERRIES, INCLUDING DEWBERRIES

EXCEPT for the Logan (Loganberry), cultivation of the blackberry is chiefly limited to North America and most varieties of blackberries have originated in this country. Hedrick (*31*) [2] states that the blackberry came into cultivation little by little early in the nineteenth century. It became more common as a cultivated fruit about 1850, when several selections from the wild were introduced into cultivation. Among these was the Lawton, which is still grown. The Snyder variety was introduced about 1860, the Eldorado before 1891, and the Lucretia trailing blackberry or dewberry about 1875. These, as well as almost all others that have been grown commercially, were selections from the wild. Wilson Junior, raised from seed of Wilson Early, and Minnewaski, grown from seed at Marlboro, N. Y., have resulted from efforts to improve this fruit in Eastern States, but neither variety is now grown commercially to any extent.

In the West, efforts to improve the blackberry have met with much greater success. Selections of the wild trailing blackberry were first grown. Among these was the Aughinbaugh. In 1881, J. H. Logan raised the Logan and probably the Mammoth from seed of the Aughinbaugh. A second generation was raised from some of the seedlings, and from these the Black Logan and other promising varieties were selected. The Logan is still important, but the Mammoth is only occasionally grown now. The Black Logan may possibly still be raised, either as Black Logan or under other names. In 1897 Luther Burbank introduced the Phenomenal, very similar to the Logan. This was widely grown for a while, but it has largely disappeared.

About 1926 the Young dewberry (Youngberry) or trailing blackberry was introduced. This is a hybrid between the Phenomenal and the eastern Mayes dewberry (Austin Mayes), made by B. M. Young, of Louisiana. In 1935 the Boysen (Boysenberry), very similar to the Young, was introduced. Its origin is unknown.

In Oregon, Washington, and New Jersey the Evergreen or Black Diamond is cultivated. It is a very old variety from England that has

[1] Many experiment station workers and private breeders have contributed records and information. To these the writer is most grateful. Among those especially generous of their time were George L. Slate and L. M. Cooley (New York), J. H. Clark (New Jersey), A. S. Colby (Illinois), E. Angelo and A. N. Wilcox (Minnesota), C. F. Williams (North Carolina), and George F. Waldo (Oregon). W. J. Strong, M. B. Davis, N. H. Grubb. C. G. Dahl, and P. Stedje contributed information on work at foreign stations. B. M. Young (Louisiana), H. Rockhill (Iowa), W. E. Lammertz (California), and George Pyne, of Topham, Devon, England, have all contributed information.

[2] Italic numbers in parentheses refer to Literature Cited, p. 523.

become widely naturalized west of the Cascade Mountains in Oregon and Washington. In California, and to a slight extent in Oregon and Washington, the Himalaya (*Rubus procerus* P. J. Muell.) is raised. This is considered identical with the Theodor Reimers variety of Germany. It also is widely naturalized west of the Cascade Mountains Besides these two, several other European varieties that have been named in recent years have been tested, but no others have succeeded in the United States. In 1932 the Brainerd, a hybrid between the Himalaya and an eastern variety, was introduced. Thus, except for the Logan, Phenomenal, Young, Brainerd, and possibly the Boysen, the cultivated varieties of blackberries have originated as chance seedlings in the wild.

At present the Eldorado (Stuart) is the leading blackberry of the eastern erect type, Lucretia the leading trailing blackberry or dewberry of the eastern group, Logan and Young the leading trailing varieties of the western type. The Evergreen (Black Diamond) is the leading variety of the European type.

American Wild Blackberries and How Varieties Originated From Them

The wild blackberries of North America fall into five major groups: (1) The erect or nearly erect types, like Early Harvest (fig. 1) and Eldorado, of the eastern United States from Florida to Canada and from the Atlantic coast to the Prairie States; (2) the eastern trailing blackberries, not red-hairy caned, much like the Lucretia, having about the same range as the erect ones; (3) the southeastern trailing blackberries having red hairs on the canes, like the Manatee and Advance, ranging along the Atlantic and Gulf coasts from Delaware to Texas; (4) the trailing blackberries, from which the Logan is derived, of the Pacific coast from Canada to southern California; and (5) the semitrailing Evergreen (Black Diamond) and Himalaya

IN SPITE *of the fact that a good deal has already been accomplished, the possibilities of improving the red raspberry by utilizing the available cultivated varieties in further breeding work are still enormous. Some of the qualities, now found separately, that may be combined in raspberries of the future are the very large fruit size of European varieties and newer American productions, immense fruit clusters, great productiveness, firmness, vigor, and resistance to diseases. But there is also a large reservoir of germ plasm, hardly yet touched by raspberry breeders, in the wild species of Asia and elsewhere, some of which resemble the grape, hawthorn, bamboo, maple, and apple in their leaf forms, and vary from low and soft-stemmed plants to plants with stems 3 inches thick and 14 feet high.*

of Oregon, Washington, and California, that have been naturalized from Europe and which have become serious weeds of roadsides, pastures, and open forests. There are no native blackberries in the Rocky Mountains of the United States.

Originally, when North America was settled, most of the wild blackberries could be classified into a few relatively distinct species, and though blackberries were gathered from the wild, they were nowhere as abundant as at present. When the forests were cut and the land was cleared for pasture and meadow, the chief cover in many northern sections for several years was the wild blackberry. Birds ate the berries and dropped the seeds in the brush. These clearings of forest and pasture gave the opportunity for seedlings of different wild species to grow side by side, as they had not when dense virgin forest covered the land.

Figure 1.—**Early Harvest, derived from the eastern erect blackberry.**

Normally, the wild blackberries of the East are entirely or nearly self-sterile, and those of the Pacific coast have male and female organs on separate plants. All need cross-pollination. In the clearings and pastures bees and other insects have crossed the blackberry species for the last 100 to 300 years, and hybrid seedlings have grown up, so that immense numbers of hybrids may now be found. These hybrids vary from sterile to productive plants, and many are extremely vigorous. Backcrosses between a hybrid and one parent and crosses between hybrids are also appearing. Thus man, by clearing the forest, has started an immense breeding project. For the last 75 or 80 years man has been cashing in on this project by selecting the best of these wild hybrids and trying them under cultivation. Always he has overlooked the fact that the wild species were cross-fertilized.

Two or more selections were not planted together, so that many of the selections, when propagated by themselves under cultivation, were not productive. Furthermore, most of the wild blackberries are woodland plants, fruiting best in the leafmold at the edge of the forest and along streams. No wonder many of the selections were unproductive under cultivation. Through scores of years, however, selections of species and of hybrids have been found that have been productive when grown by themselves in open fields. In the South no productive selection that will set fruit by itself has yet been made of the trailing species with red-hairy canes. When the Rogers or Advance is grown, two or more selections are actually interplanted and cross-pollination is thus made possible, but many growers are unaware of this fact.

There is no final agreement as to just how many botanical species should be recognized, because the species have hybridized freely. Brainerd and Peitersen (*6*) list eight erect or semierect and four trailing species for New England. Canes of these species are shown in figure 2. Their survey of the wild forms was extensive and thorough and was supplemented by experiments on the effect of environment on botanical characters and by studies in hybridization. It seems best to follow their classification and viewpoint. The qualities of possible value to breeders are briefly described for several species as follows:

The "high-bush" or "black-long berry", *Rubus allegheniensis* Porter.—Canes strong, erect growing, with stout prickles; leaves mostly very large and strongly heart-shaped; clusters largest of American blackberries, 14- to 18-flowered; fruit large, long, sweet, and one of the best. Common in fields and pastures from New England to Wisconsin, but ranging from Minnesota to Nova Scotia and in the mountains to North Carolina and Tennessee. This is one of the purest and most distinct of northeastern erect blackberries. Snyder, though probably a hybrid, is close to the wild type, while Ancient Briton, Eldorado, Taylor, Agawam, Jumbo, Lawton, Stone, and Wachusett are probably hybrids of this species with others. Albino forms are fairly common in the wild.

The "tall" blackberry, *Rubus argutus* Link.—Canes very erect, deeply furrowed, prickly; clusters 8- to 12-flowered; fruit often with bitter aftertaste. This, or closely related forms, is the most common blackberry of the roadside and fields of the eastern United States. Early Harvest is close to the wild type of this species, while Erie is probably a hybrid.

The "short" or "square-fruited" blackberry, *Rubus pergratus* Blanch.—Canes tall and arching, prickly; leaves large and broad; clusters 8- to 12-flowered; fruit short, cylindric. A hardy blackberry of the higher elevations in New England, New York, and Pennsylvania, with large but short fruit of excellent flavor. It does not seem to be represented in cultivated varieties.

The "leafy-flowered" blackberry, *Rubus frondosus* Bigel.—Canes arched and recurving, prickly; leaves broad; clusters 8- to 12-flowered; fruit not so large as that of the above species. This is the common blackberry of the fields of New England, and next to *R. argutus* the most common of the blackberries of the eastern United States. It seems to thrive better than most species in the open fields. It has probably hybridized most extensively with *R. argutus*. Varieties nearest to the wild types are Joy, La Grange, Ward, and Watt, while most of the varieties listed above as hybrids of *R. allegheniensis* are probably hybrids with this species.

The "thornless mountain" blackberry, *Rubus canadensis* L.—Canes erect to arching, without prickles; leaves without hairs; leaflets long with long stalks, especially the terminal one; clusters loose; fruit long, tart. This thornless or prickleless blackberry is native to the higher mountains from Georgia northward to Newfoundland and Quebec, but is found at the lower elevations from northern Maine west to Wisconsin. It is a forest plant and does not succeed well at the lower elevations in open fields. Its fruit is excellent and the plant is very hardy northward. No variety derived from this is now under cultivation.

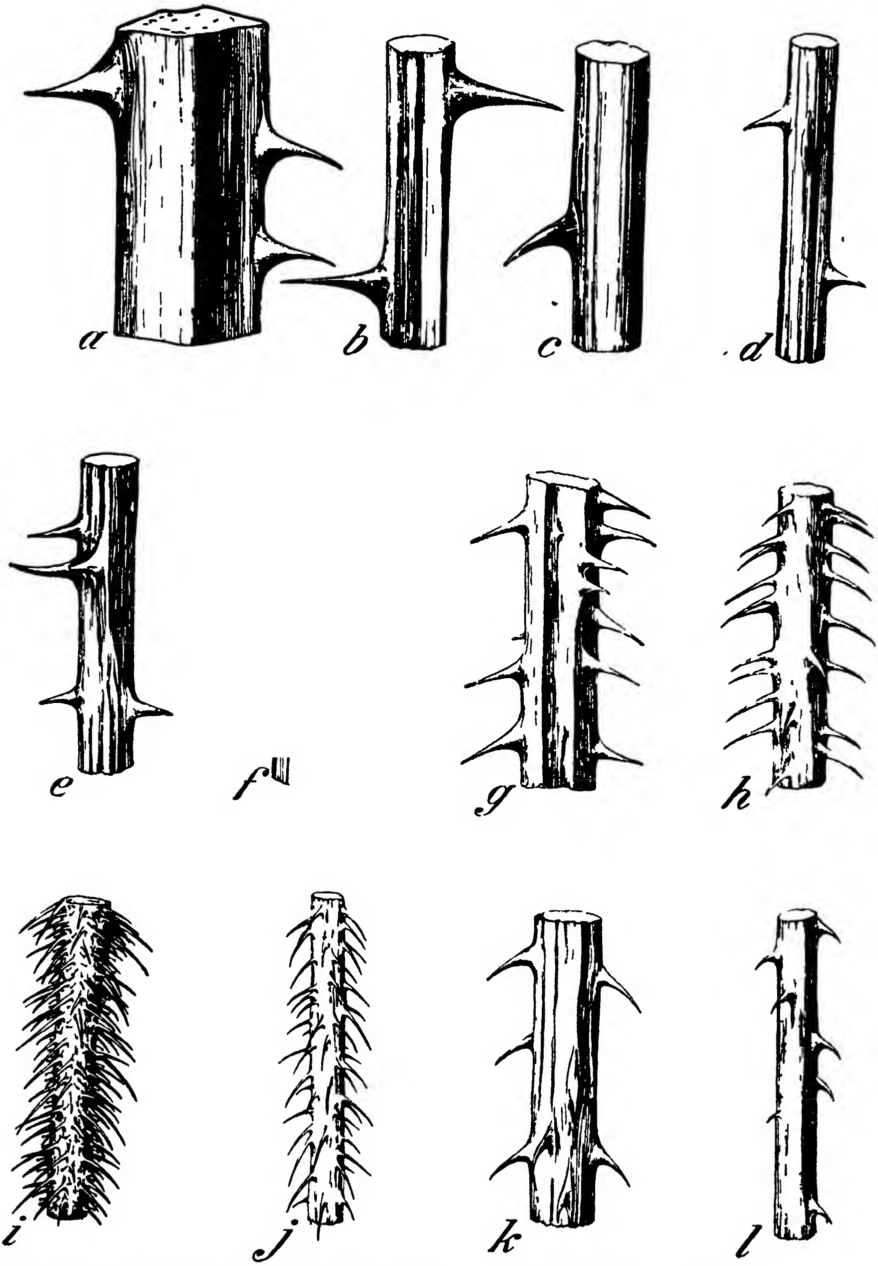

Figure 2.—Canes and prickles of 12 eastern species of the blackberry group (*Eubatus* section of genus *Rubus*): *a*, *Rubus allegheniensis*; *b*, *R. argutus*; *c*, *R. pergratus*; *d*, *R frondosus*; *e*, *R. recurvans*; *f*, *R. canadensis*; *g*, *R. elegantulus*; *h*, *R. vermontanus*; *i*, *R. setosus*; *j*, *R. hispidus*; *k*, *R. procumbens*; *l*, *R. baileyanus*. (After Brainerd.)

The "Vermont" blackberry, *Rubus vermontanus* Blanch.—A rather rare blackberry with recurving canes that has small but very numerous fruits. It is found at the higher elevations from New York to Nova Scotia and is quite hardy.

The "sand" blackberry, *Rubus cuneifolius* Pursh, is native along the coast from Connecticut to Texas and is not fully hardy in the North. It has very erect and quite thorny canes, and the fruit ripens much later than that of other American blackberries. In fact this species, with its often pink flowers, grayish foliage, and late fruit, is the closest of any to the European group of blackberries. Eureka belongs to this species, and Nanticoke is close to it.

The dewberry or trailing blackberry, *Rubus baileyanus* Britt.—Canes trailing, prickly; clusters one- to three-flowered; seeds large. This is one of the probable parents of the cultivated dewberries Mayes and Lucretia, which are probably hybrids of *R. baileyanus* with *R. argutus*. It is one of about three widely distributed trailing species in the eastern United States.

The "southern red-caned" dewberry, *Rubus trivialis* Michx.—Canes trailing, prickly, usually with dense red bristles, often evergreen; flowers large, usually solitary; fruit large, long, very early. This species, like the sand blackberry, is native along the coast from Maryland to Texas, but extends up the Mississippi Valley to Arkansas and southern Missouri. It has large, long fruit that ripens earliest of all. The Advance, Rogers, and Manatee all belong to this species. The Advance and Rogers have extremely firm fruit in several-fruited clusters and are apparently immune to double-blossom or rosette disease.[3] The limitations of the species are usually 1-flowered clusters, entire self-sterility (*24*), lack of hardiness except in the South, and prevalence of the double-blossom or rosette disease in the South.

The trailing blackberries or dewberries of the Pacific coast, *Rubus ursinus* Cham. and Schlecht., *R. macropetalus* Dougl., and *R. loganobaccus* Bailey.—Canes trailing, prickly, nearly evergreen; clusters usually 5- to 10-flowered, with sexes on separate plants; fruit to 1½ inches in length, deep wine colored to black. All three species are very subject to leaf spot and anthracnose, which limit their culture in the Eastern States. *R. macropetalus* occurs mostly in Oregon, Washington, and British Columbia, and *R. ursinus* and *R. loganobaccus* in California. All have highly flavored tart berries, the Logan being derived from *R. loganobaccus*, which occurs from about Watsonville north to the California-Oregon State line. The Young, Boysen, and Cameron derive their fine flavor from this latter species. Cazadero and other varieties have been derived from *R. macropetalus*.

The probable derivations of cultivated varieties are:

Rubus allegheniensis × *argutus:* Ancient Briton, Eldorado, Taylor.
R. allegheniensis × *frondosus:* Agawam, Erskine Park, Jumbo, Lawton, Snyder, Stone, Wachusett.
R. argutus × *frondosus:* Blowers, Erie, Mersereau.
R. baileyanus × *enslenii* Tratt.: Premo.
R. baileyanus × *argutus:* Mayes, Lucretia.
R. argutus: Early Harvest.
R. frondosus, or (*R. frondosus* × *argutus*) × *R. frondosus*· Joy, La Grange, Ward, Watt.
R. cuneifolius: Eureka, Nanticoke (possibly *R. cuneifolius* × *argutus*).
R. trivialis: Manatee, Rogers, Advance.
R. loganobaccus: Logan.
R. loganobaccus × (*R. baileyanus* × *argutus*)*:* Young, Boysen.

Great Names in Blackberry History

The important names in blackberry history include W. O. Focke; H. Sudre, E. Brainerd and A. K. Peitersen, L. H. Bailey, B. Lidforss, J. H. Logan, and B. M. Young.

Focke was a German botanist with a broad viewpoint who made the study of the systematic botany of the blackberry-raspberry group a large part of his life work. He (*25*) divided the genus into subgenera and species in an understandable way. He described 132 species of

[3] Double-blossom or rosette disease is caused by a species of *Cercosporella* fungus which infects the buds causing a rosette or witches'-broom type of growth. The infected blossoms become distorted and are sterile.

blackberries. He gave a discussion of the origin of European blackberries to which reference is made in the appendix

Sudre (*54*), a French botanist, confined himself to the European blackberries. He tried to determine the original species of Europe by a study of their distribution and relationships and of the percentage of good pollen in their flowers. He described 110 species for all Europe.

Brainerd and Peitersen (*6, 44*) worked chiefly in Vermont and elsewhere in New England. In their two bulletins on the blackberries of New England they give an understandable grouping of the wild blackberries of the eastern United States. The two men made extensive field surveys, grew the wild forms side by side under cultivation, and made many crosses and many experiments on the effect of climatic conditions on the different forms. They describe 12 species for New England and refer many of the cultivated varieties to the species or their hybrids. Experiments in shading parts of plants showed that leaves of plants in heavy shade had less than one-seventieth the number of hairs and far fewer prickles than leaves in the sun. Canes in the shade were trailing, but those in the open were erect. The work showed (1) that the species of eastern North America and most hybrids were self-sterile or nearly self-sterile; (2) that hybrids had a large percentage of aborted pollen; and (3) that the hybrids showed segregation.

Figure 3.—B. M. Young, of Morgan City, La., at about the time he originated the Young dewberry (Youngberry) over 30 years ago. Mr. Young is still breeding raspberries and blackberries.

Bailey (*3, 4, 5*) has compiled much information regarding the history of both the cultivated and the wild blackberries and has made extensive field collections of both. He has issued a series of monographs on his interpretation of the wild species and has described many new forms.

Lidforss's studies (*34*) on inheritance in European blackberries, which were published in 1914 after his death, furnish an account of the development of the wild European blackberries. He obtained true and false hybrids in crosses and in selfing. The true hybrids always split in the second generation, while the false hybrids reproduce the mother exactly. In the false hybrids (1) no seed development occurs without pollination; but (2) when the flowers are pollinated false seed develops; (3) this false seed apparently does not develop from the ovule but from a cell in the wall of the ovary; and (4) the plants grown from such false seed are just as like the mother plant as if

propagated from a rooted tip or a root cutting. Gustafsson (*28*) also studied the development of false hybrids. Some European forms produce these false seedlings only; others may produce some true and some false, while others produce all true seedlings. Thus in Oregon and Washington the Evergreen and Himalaya blackberries usually reproduce each other exactly from these false seeds, and hundreds of thousands of wild plants occur that are just as alike as if they had been propagated by root cuttings or by tip plants (*20*). Only rarely are true seedlings of these two varieties found.

B. M. Young, of Morgan City, La. (fig. 3), produced a hybrid between the Phenomenal (very similar to Logan) and the Mayes

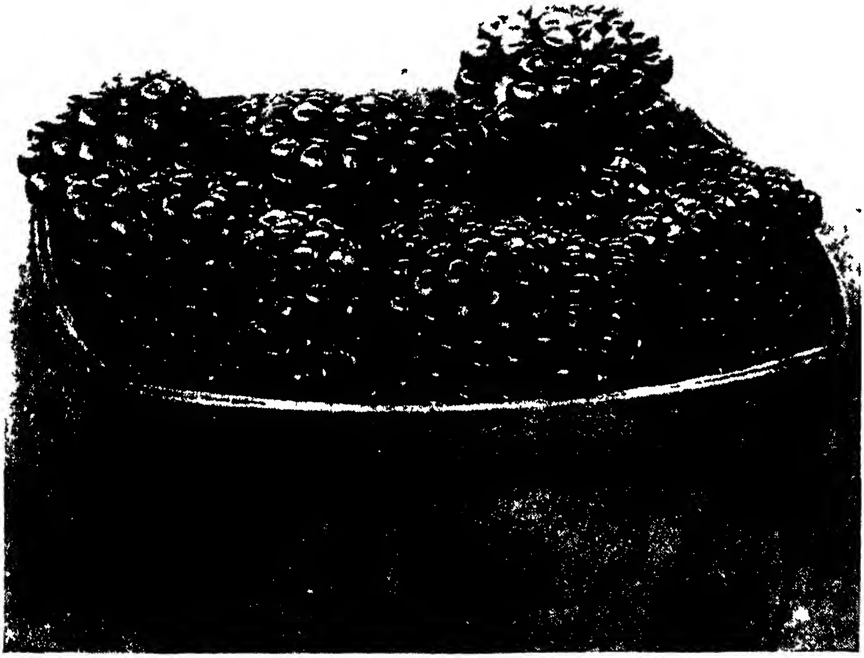

Figure 4.—The Young dewberry or trailing blackberry (Youngberry), one of the finest-flavored, largest, and most productive varieties; a cross of Phenomenal × Mayes.

dewberry or trailing blackberry about 1905. It was not introduced until about 1926, but it has quickly become an important sort (Young dewberry, or Youngberry, fig. 4), replacing the Logan to a large extent in California and to some extent in Oregon and Washington. In regions to which it is adapted it is the finest in flavor of all the blackberry group. Though Young has done extensive berry work since then, he has introduced no other variety.

The Logan and Its Relatives

The origin of the Logan is not yet fully explained. As stated above, in 1881 Judge Logan, at Santa Cruz, Calif., grew seedlings of a very rank-growing trailing blackberry, the Aughinbaugh. It was

pistillate-flowered, so that the flowers must have been pollinated either by wild male blackberries nearby, by an eastern erect blackberry in his garden, or by a red raspberry. Among about 100 seedlings there was the one later named Logan (fig. 5) with large, deep-red fruits. Judge Logan assumed that it was a cross of the black-fruited Aughinbaugh with the red raspberry. In recent years several facts have thrown doubt on this: (1) Blackberry-raspberry hybrids are mostly sterile, and if they do fruit they neither pick off like the blackberry nor pull off like the raspberry, but mash in the hand, while the Logan picks off like a blackberry. (2) Seedlings of the Logan

Figure 5.—The Logan blackberry (Loganberry), derived from the western trailing blackberry.

are all red-fruited and pick off like a blackberry. They vary in size, sweetness, season of ripening, vigor, etc., but show no distinct raspberrylike characters. (3) Cytologically the Logan seems like a pure species (*22*). Chromosome pairing is regular and reduction division is quite normal as for a pure species, not abnormal as in hybrids. It has 42 chromosomes, while the raspberry has 14. Plants of the species nearest like the Logan have 42 as the most common number. (4) Many hybrids of the Logan with selections of the wild blackberry are fertile, while most crosses of the Logan with the raspberry are not.

On the other hand, blackberry-raspberry hybrids resemble the Logan in habit of growth and to some extent in type of fruit. The red-fruited wild blackberries of the Pacific coast so far observed are much lighter red than the Logan. Perfect-flowered self-fertile selections of the wild observed so far differ considerably from the Logan.

Further study of the wild blackberries of the West, as grown under cultivation, and hybrids with the red raspberry and blackberry should do much to unravel the origin of the Logan. The evidence at hand indicates that the Logan is most probably a red-fruited sport of the wild blackberry.

Evolution of the Blackberries of Europe

There are two great centers of wild blackberries, eastern North America and Europe. According to Focke (*25*), the European and American species were separated in comparatively recent time, geologically speaking, probably by the southern movement of glaciers in the ice age. He holds that there are some 15 general types with a few more species to which all European blackberries can be referred. Sudre (*54*) came to a similar conclusion. Gustafsson (*28, 29*), of Sweden, concluded that when the ice age brought two widely different species groups together so that they hybridized, many of the pseudogamic blackberries of Europe that come true to seed originated. Because they came exactly true to seed they could reproduce themselves down through hundreds and thousands of years and eventually became widely distributed. ✓ At the present time in Europe there are thousands of forms of blackberries. Some few are good species; more are ancient hybrids that are more or less widely distributed; and many others are pseudogamic forms resulting from hybridizing, of which Oregon Evergreen and Himalaya are representative in this country. The Brainerd (*23*), which originated as a cross of Himalaya and an American variety, reproduces to some extent by pseudogamy, though no purely American variety is known to reproduce in this way.

Crane refers to *Rubus thyrsiger* Banning and Focke, *R. nitidioides* Watson, *R. borreri* Bell Salt., *R. laciniatus* Willd. (Evergreen), *R. rusticanus* E. Merc. and its variety *inermis* Willd., *R. schlechtendahlii* Wiehe, *R. calvatus* Blox. (Edward Langley), and *R. procerus* (Himalaya) as being European blackberries of possible value for breeding, *R. thyrsiger* and *R. nitidioides* have very large clusters of good-sized fruit of excellent flavor. *R. borreri* is early for a European blackberry. *R. rusticanus* is late and small-fruited, but hybrids are cultivated varieties. *R. inermis* is a thornless form of *R. rusticanus*.

Thornless Sports of Blackberries

Productive thornless sports of the Evergreen, Logan, Mammoth, and Young have been found, propagated, and introduced. Bud sports in general are considered to be due to the appearance of recessive characters, and this is probably the case with these blackberries. However, these productive thornless sports are all chimeras, having a thin layer of thornless tissue overlying thorny. Whenever they are propagated by root cuttings, or when the canes freeze back so that shoots come up from below the crown, they are always thorny. Seedlings of the thornless Evergreen raised by the writer, and seedlings of other thornless sports raised by H. M. Butterfield, of the University of California, have all been thorny.

Most thornless sports have been unproductive, and thornlessness may be linked with sterility (*19*). For a thornless sport to be productive the thornless tissue around the outside of the cane apparently

should be thick enough to prevent the production of thorns, but not thick enough to form the tissue that produces flowers and berries. If the thornless layer is relatively thick so that flowers are produced from it, then the flowers seem to be entirely or nearly sterile.

Breeding Work at Experiment Stations

Compared with other berries, little systematic breeding work has been done with the blackberries. The aims of experiments now under way probably represent some of the most worth-while objectives.

At the Rhode Island Agricultural Experiment Station the origination of hardy thornless forms is being studied. The first crosses were made in 1929. Thornless sorts such as *Rubus canadensis*, Austin Thornless, Cory, and Thornless Young have been crossed with Snyder, Eldorado, Alfred, Lucretia, and Gardena.

At the New York (State) station the first crosses were made in 1912, and some have been made from time to time ever since, notably a considerable number in 1927. Eldorado has been crossed with Agawam, Rathbun, Joy, Best of All, Brewer, Buckeye, and Erskine Park; Erskine Park with Rathbun and Buckeye; Rathbun with Agawam and Snyder. Agawam has been selfed and crossed with Snyder; Buckeye with Joy; Mersereau with Snyder. Strawberry Flavored has been selfed. The Eldorado × Brewer cross is considered a good one.

At the North Carolina station dewberry breeding began in 1926. Young and Lucretia were crossed, and the first-generation selections have been backcrossed in an attempt to obtain productive, disease-resistant, high-flavored, thornless sorts. The Cameron variety has been selected, propagated, and named for its vigor, high flavor, firmness, thornlessness, and resistance to anthracnose, to septoria leaf spot, and to nematodes, and D-3 and D-4 for the size of their cluster. In a cross of Young × Austin Thornless there were 334 thornless and 411 thorny in the first-generation progeny.

At the Texas station breeding work began in 1909. Ness (*41*) crossed a selection of the southern dewberry, *Rubus trivialis*, with the Brilliant red raspberry in 1912. The first and second generations were quite sterile except for five of the second-generation (open-pollinated) plants. These gave rise to a third generation, from which selections were made that were introduced as Nessberry in 1921. The Nessberry was then backcrossed with the dewberry, two raspberries, and a blackberry. The resulting progenies have been selfed for two to four generations.[4] The Nessberry is drought-resistant and has high flavor, but the fruit does not separate from the stem like either a blackberry or a raspberry. The obtaining of fertile seedlings in the third and fourth generations indicates that it may be possible through backcrossing to obtain seedlings the fruit of which will separate either like a raspberry or like a blackberry. Other breeding begun by Yarnell in 1934 (*57*) involves crosses and selfing of Young, Early Harvest, Hall Lawton, Crandall Early, Early Wonder, Lucretia, Dallas, Haupt, and Mayes.

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[4] S. H. Yarnell (*57*), who has carried on the work in recent years, found that the Nessberry ($n=14$) has twice the chromosome number of its parents ($n=7$), and he concluded that its fertility was due to chromosome doubling. Plants of the F_3 of Nessberry ($n=14$) × Hallsham red raspberry ($n=7$), and plants of the F_4 of Nessberry × Early Harvest blackberry all had the 14 ($2n=28$) chromosome number and were fertile.

Breeding Work of the United States Department of Agriculture

The first crosses in the blackberry-breeding work of the United States Department of Agriculture were made in gardens in Atlanta, Ga., in 1919, and the seedlings were raised at Glenn Dale, Md. Only two seedlings grew to maturity, one of which was named the Brainerd (fig. 6) (*23*). It is a cross of Himalaya with an erect garden variety, probably the Georgia Mammoth The Brainerd is grown commer-

Figure 6.—The Brainerd blackberry, a cross of Himalaya on an erect-growing eastern variety. Note the large clusters of this variety. It is being grown in western Oregon for shipping and canning.

cially at Gresham, Oreg., for canning and shipping, replacing Himalaya for that purpose. It was hardy in Maryland until the winters of 1934–35 and 1935–36, when it was injured by temperatures of −17° and −23° F. Later crosses made at Beltsville, Md., and Willard, N. C., were between cultivated varieties such as Joy, Eldorado, Jumbo, Mersereau, and Blowers, while Eldorado and Joy were selfed. Recent crosses have been between Himalaya and Evergreen, Joy, Snyder, Early Wonder, Austin Thornless, Taylor, Lawton, and Eureka. The objective is to combine the size of fruit and hardiness of eastern varieties with the productiveness and vigor of the Himalaya. In these crosses a large proportion of the first-generation hybrid plants are true Himalaya, due to the development of "false" seedlings in this variety of the European type. In the crosses of Himalaya with American varieties 64 percent were maternal, that is, just like Himalaya, and 36 percent were true hybrids. In the cross Himalaya × Thornless Austin, about half of the true seedlings are thornless.

The breeding work at Corvallis, Oreg., is chiefly directed toward combining the high flavor of the native trailing blackberry with the size, firmness, productiveness, and hardiness of commercial varieties. Selections of different types of the wild blackberry, as well as the Logan, Young, Ideal Wild, and Zelinski, have been used in crossing with one another and with Lucretia, Austin Thornless, Eldorado, Oregon, Evergreen, Himalaya, and Mammoth. Crosses of the Logan with Mammoth, Lucretia, and Young were mostly sterile (*22*), even though they have the same chromosome number. Many selections have been made from the wild and Logan crosses, some having the high flavor of the wild, which is considered the highest quality in all the dewberry-blackberry group. One Himalaya × Logan hybrid is fully fertile and fairly vigorous, the second generation showing segregation into an immense number of forms. Out of a population of 817 hybrids of Logan × Young, 2 very firm-fruited selections have been made, both having the deep wine-colored fruit of the Young.

Blackberry-Raspberry Hybrids in England

Besides the Nessberry discussed above, several hybrids between blackberry and raspberry have been raised in England. Among these are Laxtonberry (Logan × Superlative), Mahdi (Belle de Fontenay × common English blackberry), Veitchberry (November Abundance × common English blackberry), and Kings Acre. The Mahdi and Kings Acre have 21, Veitchberry has 28, and Laxtonberry 49 chromosomes in vegetative cells. The Veitchberry is the most fertile and productive. None of these hybrids, however, has proved of commercial value, though they are of good quality. Just as with the Nessberry, they do not separate readily from the stem like either a raspberry or a blackberry. Possibly they will need to be backcrossed with a raspberry or with a blackberry before seedlings can be obtained that produce fruit that can be picked readily. Gruber (*27*) in Germany is doing some work in crossing blackberries and raspberries to transfer the disease resistance of the blackberry to a raspberry.

Some Problems and Objectives of Blackberry Breeders

Among the most important objectives for breeders are hardier northern varieties, thornlessness, small seed, high flavor, firmness, and resistance to double blossom and orange rust. Sources of each of these desirable characters are known and are listed in the appendix. Thus, both *Rubus canadensis*, the thornless blackberry, and *R. pergratus* are native in northern regions where most cultivated varieties are not hardy. Austin Thornless, Burbank Thornless, Cameron, and *R. canadensis* are available for breeding thornless varieties. With their superior flavor, *R. pergratus* and *R. allegheniensis* for eastern and *R. macropetalus*, *R. ursinus*, Logan, Young, and Boysen for western blackberries furnish material for great improvement in dessert quality. Excepting *R. cuneifolia*, the most erect blackberries have the smallest seeds, though a large-fruited and large- but few-seeded trailing variety like the Young may not be objectionably seedy.

It may be possible to utilize some of the immense-fruited blackberries of northern South America in breeding (*45*). They belong to a very different group from North American blackberries; but it is possible that hybrids with this group might be large-fruited seedlings that would reproduce exactly from seed, as do certain European varieties resulting from wide crosses.

RASPBERRIES

History of the Raspberry

According to Hedrick (*31*), the first red raspberries were introduced into cultivation in Europe about 400 years ago. Three hundred years ago there were at least two varieties cultivated in England, but variety names were not applied until after 1800. The European varieties were introduced into the United States even before 1800 and at first were raised even more extensively than were selections of native American raspberry. Probably one or more selections of the American red raspberry were in cultivation by 1800. The first named black raspberries were probably the Doolittle, introduced by H. H. Doolittle, Oaks Corners, N. Y., about 1850, and the Ohio Everbearing, found by Nicholas Longworth, Cincinnati, Ohio, in 1852.

A Dr. Brinkle, of Philadelphia, Pa., was the first successful raspberry breeder of this country. He originated many varieties of raspberries, among which was the high-flavored Orange (Brinkles Orange). This he raised from seed in 1845. Although there was a considerable acreage of raspberries around some of the larger cities, it was nearly 1870 before the raspberry became a crop of any great importance. The Cuthbert variety was found as a chance seedling in 1865 in what is now a part of New York City; it was probably a cross of Hudson River Antwerp, a European variety, with a wild native red. Ever since the introduction of the Cuthbert, which is still the chief variety of the Northwest, the raspberry has been an important small fruit. Cuthbert and Ranere (St. Regis) are the only important varieties of red raspberry now grown that originated as chance seedlings.

Other leading red raspberries are Latham, Chief, Ohta, Marlboro, and King, all of which resulted from definite attempts to improve the

raspberry. The Marlboro was originated by A. J. Caywood, Marlboro, N. Y., before 1880, and at one time was the leading variety. The Latham originated at the Minnesota Fruit Breeding Farm as a cross between King and Loudon, and was introduced in 1912. Since then it has become the leading variety east of the Rocky Mountains. The Ohta, Chief, June, and Newburgh are other varieties from experiment stations that have succeeded.

✓ The leading black raspberries, Cumberland in the East and Munger in the Northwest, both resulted from growing seedlings, the Munger coming from seed of the Shaffer Purple. Quillen, an anthracnose-resistant variety grown in the Midwest, resulted from a cross between Cumberland and Hopkins. The other black raspberries grown to any extent commercially originated as chance seedlings. Recently, however, the New York (State) Agricultural Experiment Station, at Geneva, has introduced four black raspberries that seem to be succeeding.

The most important of the purple varieties, Columbian, was grown from seed of Cuthbert. Recently the Potomac and Sodus purple varieties have been introduced. Both are succeeding and are adapted to a wider range of conditions than Columbian. The Potomac is one of the hardiest of all raspberries.

American and European Raspberries

The commercial cultivated raspberries of the world have come from the wild red raspberry of Europe (*Rubus idaeus* L.) and the red (*R. strigosus* Michx.) and black (*R. occidentalis* L.) wild raspberries of North America (*16*).

Rubus idaeus is native in much of Europe, but closely allied forms occur across northern Asia to Japan. It is much like the North American red raspberry, but in general is not so hardy and usually has stout purple prickles, larger leaves, and duller and more conical berries. The largest size in cultivated berries has come from the Lloyd George and Pynes Royal varieties, which are derived from this species.

The American red raspberry, *Rubus strigosus*, is native in the mountains from Georgia to Pennsylvania and in both lowlands and mountains from Maine to the Dakotas, far north in Canada, and west to British Columbia. Allied forms occur in the Rocky Mountains. It has much greater hardiness than the European species, the canes are more slender and often more erect, the prickles are not so stout and sometimes are absent. The berries are seldom thimble-shaped and are usually bright red. The species is extremely variable in the wild.

The American black raspberry, *Rubus occidentalis*, has much the same range in the United States as *R. strigosus*, but ranges as far south as Oklahoma, Atlanta, Ga., and the lowlands of Virginia. It is not so hardy as the wild red raspberry, and although found from North Dakota and Quebec to Maine and New Brunswick, is far less common than the red raspberry toward its northern limit. A closely allied species, *R. leucodermis* Dougl., occurs from British Columbia to California.

The black raspberry has a sweeter but a more seedy fruit than the red. Curiously, though, yellow- or amber-fruited black raspberries

are common, and yellow and amber colors are common in the red raspberries of Europe, these colors are rarely found in American wild red raspberries. Natural hybrids between the black and the red, called purple raspberries, occur quite commonly in some sections. The purple raspberries are more vigorous and if fertile are more productive than either the red or black. The fruit is often larger and usually has more pulp or flesh in proportion to the seed.

Related berries that are often called raspberries are the two flowering raspberries of the woods, *Rubus odoratus* L. and *R. parviflorus* Nutt., with large, showy, purplish-red and white flowers and soft, thin-fleshed berries; the salmonberry, *R. spectabilis* Pursh, a perennial-caned tender species of the Pacific coast with large berries not in clusters; and the baked-apple berry, *R. chaemaemorus* L., of the bogs of northern Canada, Alaska, northern Europe, and Asia.

Future Raspberries

Three other raspberries are grown slightly in some parts of the world —the Andes black raspberry (*Rubus glaucus* Benth.) in northern South America; *R. niveus* Thunb. (*R. lasiocarpus* Sm.) in northern India and Burma; and the wineberry (*R. phoenicolasius* Maxim.), introduced from Japan, in the northeastern United States. Besides these 6 kinds, the Van Fleet, grown to some extent in the Southern States, is a cross of Cuthbert and *R. kuntzeanus* Hemsl., a Chinese raspberry (*17*).

The possibilities of improving the raspberry by utilizing just these seven species are enormous. The very large size of the varieties now in cultivation in Europe, such as Lloyd George, Pynes Royal, and the new Imperial, as well as of Marcy and many recent selections at the Geneva, Corvallis, and Puyallup stations, would hardly have been thought possible 10 years ago. Some of the qualities to be combined in raspberries of the future are the firmness of the Newburgh, U. S. D. A. No. 9 (Latham × Ranere), and Potomac; the vigor of Van Fleet; the productiveness of plants of Dixie and Van Fleet; the immense fruit clusters of *Rubus kuntzeanus* (fig. 7); the resistance to cold of Ohta, Sunbeam, Latham, Chief, Potomac, and Sarah and some other Canadian varieties; the resistance of Van Fleet and Quillen seedlings to anthracnose; of Lloyd George and Newburgh to mosaic-carrying aphis, and of Cuthbert to verticillium wilt.

The cultivated raspberries, however, are but a small part of the raspberries of the world. Focke (*25*), in his latest book on the subject of raspberries, published some 20 years ago, described 195 wild kinds of eastern and southern Asia alone. These range from whole groups with vines and leaves much like those of the grape to others with leaves like the hawthorn, bamboo, viburnum, maple, and apple. Some have soft, others woody stems. Some are low plants, while *Rubus ellipticus* Sm., the Golden Evergreen raspberry, may have canes 3 inches in diameter and grow 14 feet high (fig. 8). Eastern Asia is the center of the wild raspberries of the world.

Some of the species of Asia and elsewhere are already being crossed. The Hawaiian station and the Armstrong nurseries are working with several forms of the Akala raspberry of Hawaii. Crosses have been made between both *Rubus biflorus* Buch., a Chinese species, and the

Figure 7.—*Rubus kuntzeanus*, a very large-clustered, vigorous species of raspberry from Asia, with red, wine, and black fruit. The Van Fleet resulted from a cross between this species and Cuthbert.

salmonberry, *R. spectabilis*, and red-raspberry varieties at the Corvallis station. At the Willard and Beltsville stations and at the Tennessee station *R. kuntzeanus* of Asia and the Van Fleet are being used. At the United States Horticultural Field Station, Cheyenne, Wyo., *R. deliciosus* Torr. of the Rocky Mountains is being crossed with red raspberries. At the Beltsville and Willard stations there are about 2,000 crosses of *R. parvifolius* L. (fig. 9), an Asiatic trailing raspberry, with red, black, and purple varieties. *R. niveus* has been used by B. M. Young, of Morgan City, La., and at the Beltsville

Figure 8.—**A single plant of the Golden Evergreen raspberry, *Rubus ellipticus*, 14 feet high and 26 feet across. Some of the canes were 3 inches in diameter. (Watsonville, Calif.)**

station. William E. Whitehouse, of the Department, has succeeded recently in introducing several other species, and they are now available to breeders. The woolly raspberry, *R. lasiostylus* Focke (fig. 10), is a very large-fruited species from Asia. All the raspberry species so far studied have seven chromosomes in the reproductive cells, as have most cultivated varieties. Raspberry species so far tried in breeding have crossed readily, though many of the seedlings have not been fertile. Some of these species that have superior germ plasm of value are: For size of fruit, Akala and *R. biflorus*; for vigor of plant, Golden Evergreen (*R. ellipticus*) and *R. biflorus*; for resistance to disease, *R. biflorus*, *R. ellipticus*, *R. coreanus* Miq. (fig. 11), the Andes berry (*R. glaucus*), *R. kuntzeanus*, *R. innominatus* Moore. Most of the breeding work with raspberries lies ahead.

Raspberries and Blackberries of Unusual Colors

In the raspberry there are yellow- or golden- and apricot- or amber-colored berries as well as black, red, purple, and various shades of color from red to purple and purple to black. The yellow and apricot

colors are found in seedlings of the European red and in varieties derived in part from the European, such as Cuthbert and Herbert, but never, so far as known, from the American red. In black raspberries, the yellow form is common in the wild, especially in Maryland.

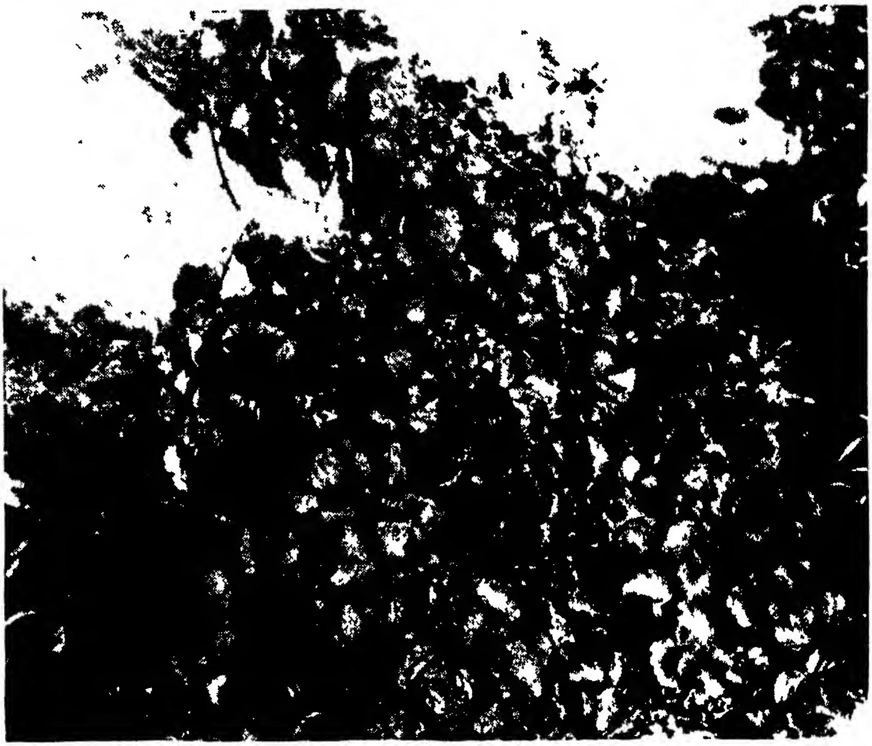

Figure 9.—Rubus parvifolius, the trailing raspberry of Japan and eastern China, which is very disease-resistant in the United States. Selections of this species are promising in southern States, and hybrids with red, black, and purple varieties are being fruited.

The introduced species of raspberries from Asia have a great variety of colors, ranging through red, orange, yellow, lavender, purple, and wine color to black.

In the blackberry, the white or pale yellow is rather commonly found in the wild in many and possibly all species in North America as well as in many species in Europe. Pink selections have been seen in Alabama and in Oregon, while lavender-colored ones have been reported in North Carolina. In the West the wild blackberry often is not quite black but a very deep wine color.

Raspberry Breeding at State Stations

At the New York (State) Agricultural Experiment Station (*50, 51, 56*) at Geneva, the first crosses were made in 1892, and the work has been continued to the present. Over 250 different crosses have been made and over 15,000 seedlings raised. Of these crosses 130 were of

red raspberries, 27 were of black raspberries, and 93 were with or for purple raspberries. For the breeding work the station maintains a collection of some 38 species of raspberries and blackberries, 33 varieties of red raspberries, 18 of black raspberries, and 7 purple varieties.

Figure 10.—Rubus lasiostylus, a very large-fruited species from Asia, the fruit of which is covered with a thick mat of hair. The upper fruit is ripe. (Natural size.)

There still are 41 station selections under test for possible introduction. Besides many commercial varieties, 55 of their own selections have been used in the breeding work, as well as the named varieties that have been introduced by the New York station.

Of the red raspberries, George L. Slate, who has had charge of the berry breeding for many years, states that Lloyd George, Newman, Herbert, and Loudon have been exceptional parents. Cuthbert has not been so good a parent, though it has transmitted its high flavor and canning quality in some crosses. Erskine Park, Buckeye, Count, Douboro, Empire, Owasco, Syracuse, Gold Drop, Ohta, Ranere, Superlative, Newman 20, and Marldon have been poor parents in the crosses made. Selfed populations resulted in dwarfs, weaklings, a high proportion of seedlings lacking hardiness, and a considerable amount of partial and complete sterility. Establishment of inbred lines has not been made a part of the breeding program because of (1) the long

time between generations, (2) the high proportion of the weaklings, dwarfs, and otherwise inferior seedlings, and (3) the difficulty of maintaining a number of inbred lines because of virus diseases, winter injury, and lack of vigor. Slate states: "The vast possibilities of improving raspberries by variety crossing make this method the

Figure 11.—***Rubus coreanus*, an Asiatic black raspberry resistant to leaf and cane diseases that is promising for breeding for southern States.**

most promising line of attack in red raspberry improvement at this station."

Many hybrids, backcrosses, and selfed seedlings have been raised involving crosses with blackberries. Among these crosses are:

Mahdi × Herbert
(Mahdi × Herbert) × (Newman × Herbert)
(Mahdi × Herbert) × Herbert
(Mahdi × Herbert) × Lloyd George
Mahdi × Phenomenal
Mahdi × Lucretia
Mahdi × Mersereau
Mahdi × (Mahdi × Lucretia)
Mahdi × *Rubus odoratus*
(Mahdi × Herbert) selfed
(Mahdi × Lucretia) selfed
(Mahdi × Lucretia) × Herbert
(Mahdi × Lucretia) × Snyder
Herbert × Logan
Cuthbert × Logan
Latham × Logan
Donboro × Logan
(Herbert × Logan) selfed
Rubus phoenicolasius × Agawam
R. phoenicolasius × Empire
(*R. phoenicolasius* × Empire) selfed
(*R. phoenicolasius* × Empire) × Empire
Smith No. 1 (black raspberry) × Snyder
Kansas × Agawam
Kansas × Mayes
Mammoth × Agawam
Mammoth × Cuthbert
Mammoth × Herbert
Mammoth × Snyder

Thus, the Mahdi, a raspberry × blackberry cross, has been backcrossed with both the raspberry and the blackberry, and the progeny

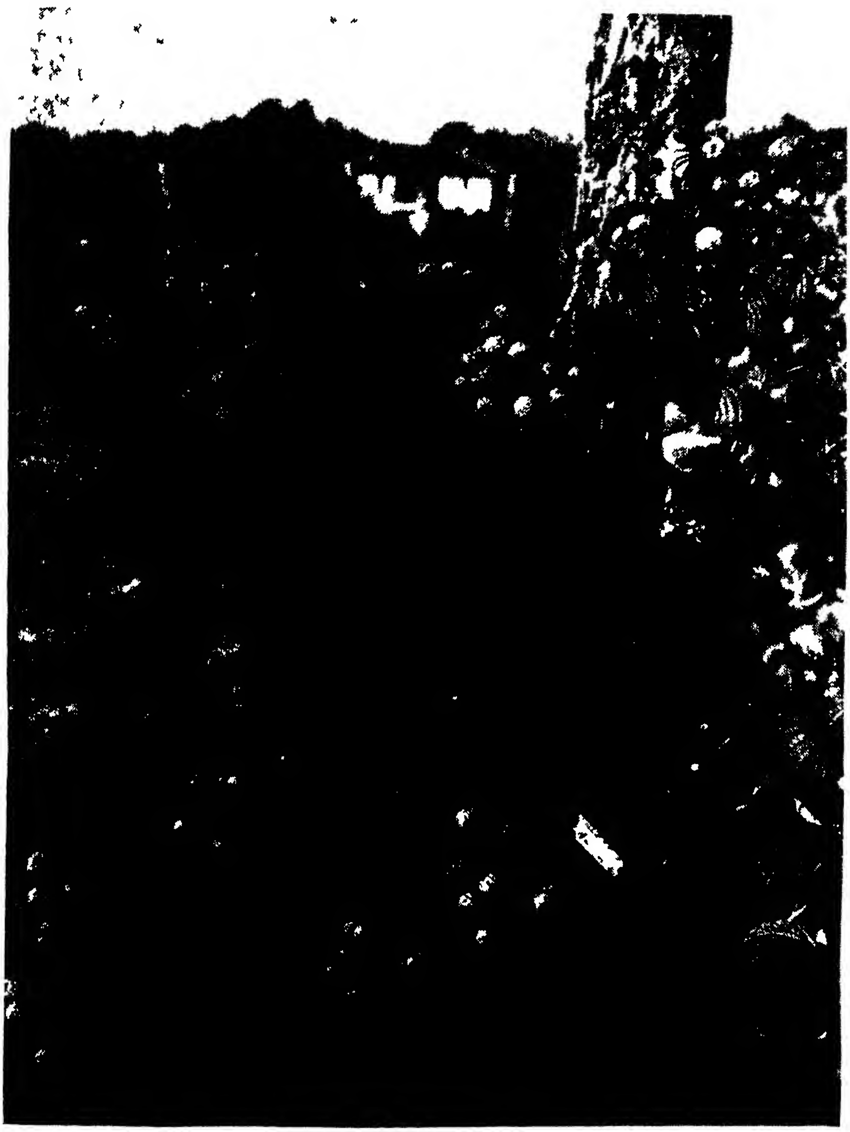

Figure 12.—A hybrid seedling with a desirable fruiting habit. Note exposed fruit, which makes picking easy.

backcrossed a second time with each. So far no selections have been introduced.

Thirty-four different crosses between the black and the red raspberries, 19 different selfings, some 21 different backcrosses with red, and 19 second backcrosses with red have been made. Over 4,300 seedlings have been raised (fig. 12), and 3 varieties have been intro-

duced, of which Brant and Sodus are first crosses and Webster is a backcross of a black and a purple. Backcrossing is still considered promising in this group. Typical red and black raspberries have not appeared when the hybrids were selfed or when purples have been crossed with purples. Dundee × Newburgh has been considered one of the most promising crosses. Besides hybrid vigor, drought resistance has been noted in the purple raspberries.

With the black raspberry, emphasis has been placed on size, color, firmness, and quality of berry, and vigor, yield, and hardiness of plant. Cumberland, Dundee, Eureka, Farmer, Grant, Gregg, Hilborn, Honeysweet, Kansas, Lane, Palmer, Rachel, Smith No. 1, and Watson Prolific have been used in crosses.

At the South Dakota station (*30*) many thousands of seedling raspberries have been grown, particularly crosses of cultivated varieties with selections of the wild red raspberry that have proved fully hardy at Brookings, with no winter protection. Sunbeam and Ohta (Flaming Giant) are two of the eight named selections resulting from the crosses that have proved to be adapted to the climatic conditions of eastern South Dakota.

At the Illinois station raspberry breeding (*1*, *2*, *8*, *9*, *10*) was begun in 1922 and over 14,000 seedlings are now under test. Some 121 selections have been made for further observations. The Quillen, Farmer, Older, Munger, and Pearl black varieties and Latham, June, Starlight, Newburgh, Ulster, and Taylor red sorts have been used in this work. Among the best crosses for purple varieties are Quillen × June, Quillen × Latham, and Quillen × Newburgh. In a study of the inheritance of anthracnose resistance, 52 percent of the selfed seedlings of Quillen were free from anthracnose, and no selfed seedlings of Cumberland, Pearl, Farmer, Honeysweet, Older, Munger, Royal Purple, Earheart, or Conrath were free. Of 661 Quillen selfed, 622 had reddish-brown canes and 34 yellow canes. Of 105 Pearl selfed, 96 had reddish-brown canes and 9 yellow, close to a 15:1 ratio. When Cumberland was selfed, all 452 seedlings had reddish-brown canes.

At the Washington State station at Puyallup raspberry breeding was first begun in 1909 (*33*). No varieties were introduced from the early work. In 1928 new breeding work was begun to obtain varieties hardier than Cuthbert, which would be satisfactory for canning, freezing, and shipping, and resistant to mosaic. Selections of Cuthbert and Lloyd George parentage are especially promising. Inheritance of fruit characters and of winter hardiness has been made an important part of the study (*48*, *49*).

At the Minnesota station the breeding work has been notable for the origination of Latham and Chief red raspberries, the Latham being the leading red variety of the eastern United States. It is estimated that at the present time there are about 25,000 acres of Latham and 3,000 acres of Chief grown. The work is being continued, and many black and red selections are now being tested. Among the principal varieties crossed are Latham, Chief, Herbert, Ranere, King, Lloyd George, Cuthbert, selections of the wild, and the Farmer and Platt black varieties. The Farmer and Platt black and the Chief red varieties have been inbred. E. Angelo, in charge of the work at

present, emphasizes the need for studies on the mode of inheritance of characters, breeding for disease resistance, and improving the flavor of the fruit.

Extensive breeding work began at the Tennessee station in 1931, using the Van Fleet for its disease resistance and vigor in the South, to cross with red varieties. Selections have been made and are being tested.

At the North Carolina station breeding was begun in 1926 to obtain varieties resistant to diseases and adapted to the South, by using Asiatic species, especially *Rubus biflorus*. One variety, Dixie, is being introduced in 1936–37. Although not large-fruited, it is one of the most productive of red raspberries and is desirable for home use. Beginning in 1936, the work was made cooperative with the Department.

Raspberry Breeding at United States Department of Agriculture Stations

The first raspberry breeding of the United States Department of Agriculture was done by W. Van Fleet while he was at the United States Plant Introduction Garden at Chico, Calif., in 1909 (*17*). He crossed *Rubus kuntzeanus*, a species from China, with the Cuthbert, and from the seedlings selected one that was later named the Van Fleet. The writer became associated with Dr. Van Fleet at the Department's station at Glenn Dale, Md., in 1920 and has carried on the breeding work since. The Potomac (purple) is the only variety introduced besides Van Fleet. The work at Beltsville, Md., and Willard, N. C., consists largely of (1) genetic studies, (2) hybridizing foreign species with cultivated varieties, and (3) crossing to obtain resistance to leaf spot, anthracnose, and leaf rust (*18*, *21*). At Willard, in cooperation with the North Carolina Agricultural Experiment Station, varieties adapted to the South are being bred, using foreign species in the crosses.

At Corvallis, Oreg., in cooperation with the Oregon station, a large part of the work is directed toward obtaining large-fruited varieties suitable for canning, freezing, and long-distance shipment. Inheritance of resistance to diseases is being studied in cooperation with the small-fruit pathologists. Red varieties used in crossing include Antwerp, Cayuga, Chief, Cuthbert, Herbert, Latham, Lloyd George, Newburgh, Ranere, and Viking; black varieties, Cumberland, Munger, and Farmer; and the purple variety, Potomac. Species used include *Rubus spectabilis*, the salmonberry, *R. leucodermis*, the western black raspberry, and several Asiatic species. Lloyd George × Newburgh crosses have been particularly promising, selections from these having larger fruit than any yet found.

At Cheyenne, Wyo., crosses are being made with the entirely hardy perennial-caned *Rubus deliciosus* in the attempt to obtain much greater hardiness.

Raspberry Breeding Abroad

Canada

Raspberry breeding was begun in Canada at Ottawa as early as 1873 (*38*), when William Saunders (*47*), later Director of the Experimental Farm at Ottawa, crossed the Doolittle (black) with the Philadelphia (dark red—a probable black × red hybrid) and obtained

24 purple-fruited seedlings. His work was transferred in 1887 to the Dominion station when he entered the Dominion service, and it has been continued since. At least 23 varieties have been introduced, of which 2, Brighton and Count, are still important varieties in Canada.

Raspberry breeding began at Vineland, Ontario, in 1913 (*43*). According to W. J. Strong, in charge of the work at present, some 125 crosses and 167 open and self-pollinations, using 16 varieties, resulted in 21,000 seedlings. About 140 selections were propagated, and one variety, the Viking, was named and introduced. This variety, introduced in 1924, is extensively grown in Ontario and is increasing slowly in importance in other sections in Canada and the northern United States. It is estimated that 1,500 acres of this variety are grown.

England

In England (*52*, *53*), extensive work in breeding raspberries by N. H. Grubb (*26*) at East Malling, Kent, has included selfing 19 varieties to study the inheritance of characters. Of 74 selfed seedlings of Pynes Royal, 22 were worthy of propagation, and of 92 selfed Lloyd George, 17 were propagated. Pynes Royal seedlings were much larger, but were mostly dark, hard to pick, and not of high flavor. Lloyd George seedlings produced many canes, but few had large fruit. Red Cross and Preussen, selfed, were very disappointing. Of 4 selections chosen for trial, all were from self-pollinated progenies of Royal × Lloyd George hybrids.

Chief emphasis has been placed by M. B. Crane and W. J. C. Lawrence (*11*, *14*, *15*), of John Innes Institute, Merton, on inheritance of characters such as sex, color of prickles and fruit, and hairiness. Two pairs of factors were found to determine sex, two color, and one hairiness.

Private Breeders of Raspberries

Several private breeders have valuable varieties to their credit, especially C. P. Newman, of La Salle, Quebec, Canada, and George Pyne, of Topsham, Devon, England. Newman (*42*) originated the Newman from seed of several varieties mixed. This variety is out-outstanding for its firmness of fruit, hardiness of cane, and mosaic resistance. It was introduced in 1919 and is still grown commercially. It is important as one of the parents of the Newburgh, Monroe, Taylor, Marcy, and Potomac raspberries.

Pyne selected Devon and Pynes Royal from self-sown seedlings and Park Lane and Red Cross from self-sown seedlings that he transplanted and tested. Mayfair came from seed of Park Lane, and Imperial from seed of Royal. Better-Late is a seedling of a blackberry-raspberry hybrid. The Red Cross is notable as an early productive sort with a long season, Park Lane and Mayfair for their high flavor, Pynes Royal for its large size, excellent flavor, and firmness, while Imperial is reported to be larger than Pynes Royal, which has been the largest raspberry known.

A third private breeder, George Adams, of Smithville, Ontario, has grown seedlings over a period of some 40 years, starting with purple and black varieties. His Adams 87 and Adams 101 are grown to a considerable extent in western New York. Adams 101 is a red variety rooting at the tips of canes, while Adams 87 is an especially hardy sort.

Generic Crosses

.Hybrids between raspberries and blackberries have been discussed above and the reported hybrids with the strawberry are discussed in the article on strawberry breeding in this yearbook. Hybrids of raspberries or blackberries with roses, apples, etc., have been reported, but no authentic cases are known. Van Fleet once stated that he had tried to cross the raspberry and a rugosa rose (*Rosa rugosa* Thunb.). He obtained sterile seedlings, which may possibly have been hybrids.

Everbearing or Fall-Fruiting Raspberries

The so-called everbearing raspberries produce a crop in the early summer at the same time as other varieties and later a second crop on the new canes. The Ranere (St. Regis) is the most common American red variety of this group. Erskine and La France are two others, and the New York (State) station has just introduced another, Indian Summer. These varieties form fruit buds on the most vigorous canes in midsummer, beginning at the tips and flowering and fruiting downward toward the base. Besides these, other varieties like the Lloyd George in Oregon and Washington begin to flower and fruit in September. Even some of the ordinary varieties such as Cuthbert may start flowering in September in some years. In the wild, fall-fruiting raspberries are often found.

Figure 13.—*A*, Red-raspberry buds and flowers. The bud at the lower left is ready to cross, or in warm, dry weather it may be so far advanced that pollen is already shedding. The other flowers are too advanced to use out of doors. *B*, After emasculating with scalpel, forceps, or the thumbnail, pollen is applied directly by twirling the flower so that the pollen is brushed from the anthers to the pistils. *C*, Blackberry flower with pistils in receptive condition and with some of the anthers on the outer stamens already split open and shedding pollen.

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Summer- and fall-fruiting black raspberries are also rather commonly found in the wild, and several have been introduced. The Ohio Everbearing was one of the first black raspberries ever named and cultivated. However, fall-fruiting black raspberries are not very practicable, for fruiting on the tips of the canes interferes with propagation. So far, only with special care have they succeeded. Purple summer- and fall-fruiting raspberries present the same difficulties as do the blacks.

TECHNIQUE OF BLACKBERRY AND RASPBERRY CROSSING

Most of the breeding work with blackberries and raspberries is done out of doors, though when tender varieties are to be used it may be done with potted or tubbed plants in the greenhouse. Flowers of

Figure 14.—Flower clusters bagged after crossing, to protect from bees.

all except self-sterile kinds should be emasculated at least 1 day before the calyx begins to split, because in some varieties under certain conditions the anthers may open and shed pollen before the buds open (fig. 13). The thumbnail is commonly used to cut away the calyx, corolla, and anthers, and the operation does not seem to injure the setting of the flowers. In the field the flower clusters should be covered with ordinary paper bags to keep insects away (fig. 14). After 1 to several days the pistils are receptive and pollen is applied. Pollen may be gathered in a dish and applied with a small, soft brush, or a flower may be twirled between the fingers so that the pollen is brushed from the stamens onto the pistils of the flowers used as the female parent. The paper bags may be taken off the flower clusters

after the third day, or, in all except the windiest or rainiest weather, they may be left on to protect the clusters until the berries ripen.

The seed of the ripe berries may be cleaned or the berries crushed in dry sand. Though dried seed of some varieties and species may germinate if given suitable conditions, they are likely to require 2 or more years. For this reason, in the work of the Department the fresh seed is planted immediately, and the flats or pots of seed are stored in a cool, moist place and are exposed the following winter to 2 or more months of cold weather just above freezing. The soil in the flats is kept moist from sowing until germination. Good germination has followed this practice. Fresh seed of tropical species generally germinates at once. Occasionally seed of some raspberry varieties has also germinated immediately after planting. Under favorable conditions the seedlings can be set in the field in the spring, and by the following year many kinds may fruit.

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APPENDIX

TABLE 1.—*Breeding work with blackberries at experiment stations*

Location	Past workers	Present workers	Year begun	Objectives
State stations:				
Georgia, Experiment	J. G. Woodroof	J. E. Bailey, H. L. Cochran, H. P. Stuckey.	1927	High-flavored southern varieties.
New Jersey, New Brunswick.		J. H. Clark	1928	Productive, disease-resistant sorts.
New York, Geneva		George L. Slate, R. Wellington.	1912	Hardy, productive sorts.
North Carolina, Raleigh.		C. F. Williams	1926	Thornless, high-flavored, disease-resistant, hardy sorts.
South Dakota, Brookings.	N. E. Hansen, Charles Haralson.			Hardy varieties.
Rhode Island, Kingston		A. E. Stene, T. E. Odland.	1929	Thornlessness.
Texas, College Station	H. Ness	S. H. Yarnell, H. F. Morris.	1908	Drought-resistant, high-flavored, productive hybrids.
Washington, Puyallup.	W. H. Lawrence, J. L. Stahl.		1909	Crosses of Evergreen and American varieties.
Department stations:				
Maryland, Beltsville (formerly at Glenn Dale).	W. Van Fleet, G. F. Waldo.	George M. Darrow	1920	Thornless productive Himalaya hybrids, Logan × eastern blackberry hybrids.
North Carolina, Willard.	G. F. Waldo	George M. Darrow, C. F. Williams.	1929	Do.
Oregon, Corvallis	C. E. Schuster, B. S. Pickett, George M. Darrow.	G. F. Waldo	1928	Thornless, firm, high-flavored hybrids of Logan, Himalaya, Evergreen, Eldorado, and selections of the wild.
Canada:				
Ontario, Lennoxville				
British Columbia, Sidney.				
England:				
Long Ashton, Bristol		J. G. Maynard, G. T. Spinks		Table and canning varieties.
John Innes Institute, Merton (*12, 13*).	W. O Backhouse	M. B. Crane, C. D. Darlington	1911	Genetics and thornlessness.
Union of Soviet Socialist Republics:				
Michurin Institute (*39, 46*).	I. V. Michurin	A. Petrov, V. G. Lithovitzer		Hardiness.

TABLE 2.—*Blackberry varieties originated by public agencies*

Location	Variety	Year introduced	Parentage	Superior qualities
State stations:				
North Carolina, Raleigh.	Cameron	1936–1937	Young × Lucretia	Disease resistant, thornless, high flavor.
South Dakota, Brookings.	Siberian	1930	Seedling of wild from Siberia.	Hardy dewberry.
Texas, College Station.	Nessberry	1921	*Rubus trivialis* × Brilliant raspberry.	High flavor, drought resistance.
Department stations:				
Maryland, Beltsville (formerly at Glenn Dale).	Brainerd	1932	Himalaya × erect eastern variety.	Vigorous, productive.
England:				
John Innes Institute, Merton.	John Innes		*R. rusticanus inermis* × *R. thyrsiger*.	Large, late, long seasons.
Long Ashton, Bristol.	Ashton Cross	1932	Seedling of wild	Large, bright, productive.
Union of Soviet Socialist Republics:				
Michurin Institute (*39*).	Abundant		Seedling of Lucretia	Hardy.

TABLE 3.—*Blackberry varieties originated by private agencies*

Name and location	Variety	Year introduced	Parentage	Superior qualities
B. M. Young, Morgan City, La.	Young	1926	Phenomenal × Mayes	Disease resistance, excellent flavor, large.
Laxton Bros., Bedford, England.	Bedford Giant	1934	Veitchberry seedling	Early for European type, large.

SOURCE OF SUPERIOR QUALITIES IN BLACKBERRIES

Plant Characters

Hardy against cold. *Rubus pergratus, R. canadensis, R. allegheniensis*, Snyder, Eldorado, Ancient Briton, Agawam.

Resistant to orange rust. Eldorado, Oregon Evergreen (Black Diamond), Russell, Snyder.

Resistant to double blossom. Himalaya, Rogers, Advance (may be same as Rogers).

Resistant to root nematode. Hall Lawton, Young, Crandall.

Resistant to crown gall. Austin Thornless, Advance.

Resistant to leaf spot (septoria). Young, Himalaya, Evergreen, Boysen, Early Harvest.

Resistant to anthracnose. Young, Boysen.

Resistant to verticillium wilt. Himalaya and Evergreen, immune; Logan and Mammoth, resistant.

Thornless (genetically thornless). Austin Thornless, *R. canadensis*, Burbank Thornless, Cameron.

Vigorous. Himalaya, Evergreen, Brainerd, Logan, *R. macropetalus, R. ursinus*, Young, Boysen; Haupt in Texas, Eldorado in North.

Resistant to drought. Nessberry.

Large flower clusters. *R. thyrsiger, R. nitidioides*, Himalaya, Evergreen.

Fruit Characters

Early ripening. Advance and Rogers (earliest), McDonald, Haupt, Lucretia, Young, Mayes, Early Harvest, Wilson Early; *R. borreri* of Europe.

Late ripening. Burbank Thornless, Himalaya, Evergreen, Brainerd, *R. cuneifolia*, Nanticoke, Eureka; *R. rusticanus* of Europe.

Firm. Oregon (Logan × Young), Advance, Evergreen; Mersereau of eastern blackberries.

Large. Boysen, Young, Mammoth, Logan, Eldorado, and Brewer.

Do not turn red in shipment.—Brainerd.

Canning. Evergreen in Oregon and Washington; Brainerd, Young, Boysen, Logan, Ideal Wild.

Freezing. Young, Boysen, Cameron, Logan.

Excellent flavor. Ideal Wild, Zelinski, Young, Boysen, Logan, *R. macropetalus* of western type; Cameron, Eldorado, Brewer, *R. allegheniensis, R. pergratus.*

Small seed. Early Harvest.

Lack of seediness. Young, Boysen.

TABLE 4.—*Breeding work with raspberries at experiment stations*

Location	Past workers	Present workers	Year begun	Objectives
State stations.				
Arkansas, Fayetteville.		J. E. Vaile	(1)	
Colorado, Loveland	R. V Lott		1930	(Work transferred to Cheyenne, Wyo., 1936)
Connecticut, New Haven.		D. F. Jones, W. R. Singleton.		Value of inbreeding.
Georgia, Experiment	J. G. Woodroof	H. L. Cochran, H. P. Stuckey, J. E. Bailey.	1927	Southern variety of high flavor.

See footnotes at end of table.

Table 4.—*Breeding work with raspberries at experiment stations*—**Continued**

Location	Past workers	Present workers	Year begun	Objectives
State stations—Contd.				
Hawaii, Honolulu		W. T. Pope	1930	Crosses with native raspberries.
Illinois, Urbana	C. J. Alexopoulus	A. S. Colby	1922	Hardiness, disease resistance, high flavor, productiveness.
Iowa, Ames				Anthracnose resistance.
Maine, Orono		R. M. Bailey	1932	
Massachusetts, Amherst.		A. P. French	1934	Isolation of pure lines for later work.
Minnesota, Excelsior	Charles Haralson, M. J. Dorsey, J. H. Beaumont, S. B. Green.	W. H. Alderman, E. Angelo, F. E. Haralson.	1891 [1]	Hardiness.
New York, Geneva	S. A. Beach, O. M. Taylor, W. H. Alderman, R. D. Anthony, M. J. Dorsey	George L. Slate, R. Wellington.	1892	Disease resistance, fall fruiting, size of fruit, quality, productiveness.
North Carolina, Raleigh.		C. F. Williams	1926	Obtaining hybrids with Asiatic species for South.
North Dakota, Fargo		A. F. Yeager, D. H. Scott.	1920	Hardiness.
Ohio, Wooster	P. Thayer (*55*)			Genetics of yellow color.
South Carolina, Clemson College.	W. J. Young			
South Dakota, Brookings.	Charles Haralson	N. E. Hansen	1898	Hardiness.
Tennessee, Knoxville.	J. A. McClintock	B. A. Drain	1931	Better varieties through use of Van Fleet and *Rubus kuntzeanus*.
Washington, Puyallup.	M. B. Hardy, J. L. Stahl, W. H. Lawrence.	C. D. Schwartze	1909 [3]	Hardiness, mosaic resistance, adaptation to canning, freezing, and dessert.
Department stations:				
Wyoming, Cheyenne.		LeRoy Powers	1935	Resistance to cold and drought. Crossing *R. deliciosus*.
Maryland, Beltsville	G. F. Waldo	George M. Darrow	1920	Disease resistance, hybrids with species, genetic studies.
North Carolina, Willard.	do	George M. Darrow, C. F. Williams (cooperator of North Carolina station).	1929	Do.
Oregon, Corvallis	C. E. Schuster, B. S. Pickett, G. L. Rygg, G. M. Darrow.	G. F. Waldo	1928	Large-fruited, hardy, canning, and freezing varieties, hybrids with species.
Canada:				
Ottawa	William Saunders, W. T. Macoun, A. J. Logsdail, John Craig.	M. B. Davis, W. Hunter.	1873 [4]	Hardiness.
Agassiz, British Columbia.				
Vineland, Ontario	F. S. Reeves	W. J. Strong, E. F. Palmer.	1913	Disease-resistant, canning, large varieties, earliness, hardiness, yield, high flavor.
England:				
Long Ashton, Bristol		J. G. Maynard, G. T. Spinks.		Table and canning varieties.
East Malling, Kent		N. H. Grubb		Disease resistance.
Merton, John Innes Horticultural Institute.		C. D. Darlington, M. B. Crane, W. J. C. Lawrence, Faberge.	1920	Blackberry-raspberry genetics.
Sweden: Alnarp		C. G. Dahl	1930	High flavor with suckers.
Norway: Njos, Hermansverk.		P. Stedje	1930	
Switzerland: Wadenswil Experiment Station.				

[1] Recently.
Or earlier.
[3] About.
[4] Official since 1887.

TABLE 5.—*Raspberry varieties originated by public agencies*

Location	Variety	Year introduced	Parentage	Superior qualities
State stations:				
Alaska, Sitka	Bensonberry	1920	Cuthbert × Salmonberry.	Perennial canes, suckers, light-yellow fruit.
Minnesota, St. Paul	Latham	1914	King × Loudon	Hardy, productive, large, attractive, late, firm.
	Chief	1930	Latham Selfed	Cold-resistant, high flavor, early, productive, vigorous, bright red.
North Carolina, Raleigh.	Dixie	1936–37	*Rubus biflorus* × Latham	Productive, disease resistant.
North Dakota, Fargo	P-117	1935	(Latham × Farmer) F_2	Cold-, drought-, and red-spider resistant, purple.
New York, Geneva	Red:			
	Donboro	1908	Loudon × Marlboro	Bright red.
	Louboro	1908	do	
	Marlative	1908	Marlboro × Superlative	Attractive.
	Marldon	1908	Marlboro × Loudon	
	June	1909	Loudon × Marlboro	Bright red, very early, productive.
	Ontario	1918	N. Y. 94 (Superlative × Loudon) selfed.	Very early, bright, productive.
	Cayuga	1922	June × Cuthbert	Earlier, firmer, brighter than Cuthbert.
	Owasco	1922	do	Large, high flavor.
	Seneca	1922	do	Late, high flavor.
	Newburgh	1929	Newman × Herbert	Very large, firm, productive, mosaic-escaping.
	Monroe	1932	Newman × Cuthbert	Midseason, firm, good.
	Ulster	1933	Herbert × June	Early, large, productive.
	Taylor	1935	Newman × Lloyd George	Large, late, firm, bright-red, high flavor.
	Indian Summer	1936	1950 (Empire × Herbert) × Lloyd George.	Fall fruiting, large.
	Marcy	1936	Lloyd George × Newman.	Very large, good flavor, mosaic-escaping.
	Black.			
	Dundee	1927	Smith No. 1 × Palmer	Large, attractive, high flavor.
	Naples	1931	Honeysweet × Rachel	Late, firm.
	Bristol	1934	Watson Prolific × Honeysweet.	Early, firm, high flavor.
	Evans	1935	do	Early, attractive, high flavor.
	Purple:			
	Brant	1926	Smith No. 1 × June	Large, firm, attractive.
	Webster	1926	Smith No. 1 × unknown purple.	Firm, productive.
	Sodus	1935	Dundee × Newburgh	Firm, large, productive, attractive.
South Dakota, Brookings.	Sunbeam	1906	Shaffer × Cavalier wild	Hardy.
	Ohta	1912	Cavalier wild × Minnetonka.	Late, firm.
	Fewthorn	1922	Minnetonka × Black Hills wild.	Few prickles, firm.
	Moonbeam	1922	(Cavalier wild × Black Hills wild) × Shaffer	Late, firm.
	Smoothcane	1922	Black Hills wild × Minnetonka.	Firm, thornless.
	Spineless	1922	Cavalier wild × Loudon	No prickles.
	Starlight	1922	Cavalier wild × Minnetonka.	right, large.
	Twilight	1922	Seedling of wild or hybrid with cultivated.	Light red.
U. S. D. A. station:				
Maryland, Glenn Dale.	Van Fleet	1924	*Rubus kuntzeanus* × Cuthbert.	Vigorous, disease-resistant, hardy in South.
	Potomac	1932	Farmer × Newman	Disease-resistant (resistant to streak virus), purple, hardy, jam and canning.
Canada:				
Ottawa	Saunders	1880	Philadelphia × McCormick.	Dark red.
	Sarah	1893	Seedling of Shaffer	Suckers, very late, firm, high flavor.
	Carleton	1894	Seedling of Biggar	Early.
	Citizen	1894	Gregg × Cuthbert	Purple, suckers.
	Count	1894	Seedling of Biggar	Early, vigorous, large, bright-red, firm.

TABLE 5.—*Raspberry varieties originated by public agencies*—Continued

Location	Variety	Year introduced	Parentage	Superior qualities
Canada—Continued.				
Ottawa	Craig	1894	Unknown	Midseason.
	Duncan	1894	Gregg × Cuthbert	Purple, suckers and tips, late, vigorous, firm.
	Empire	1894	Seedling of Biggar	Early, vigorous, firm.
	Garfield	1894	do	Firm.
	Garnet	1894	Seedling of Philadelphia.	Purple, suckers, late, vigorous.
	Lady Ann	1894	Seedling of Biggar	Yellow.
	Mary	1894	Unknown	
	Muriel	1894	Seedling of Biggar	Vigorous, early.
	Sharpe	1894	do	Early, firm, vigorous.
	Sir John	1894	do	Early, bright-red.
	Trusty	1894	Unknown	Late, firm, vigorous.
	Deacon	1900		Deep red.
	Henry	1900		Early, hardy, productive.
	Nelson	1900		Deep red.
	Lorne	1900		Early.
	Shinn	1900		Firm, productive.
	Brighton	1900	Unknown	Hardy, deep red, very early.
	Percy	1900	Gregg × Cuthbert	Purple, firm.
Vineland, Ontario	Viking	1924	Cuthbert × Marlboro	Vigorous, high flavor, productive, firm.
Union of Soviet Socialist Republics:				
Michurin Institute	Tekhas Productivnaia.	1905[1]	Seedling of Logan	Hardy, tip-rooting.

[1] Selected.

TABLE 6.—*Private raspberry breeders*

Name and location	Varieties	Year introduced	Cross	Desirable qualities
United States:				
W. E. Lammertz, Armstrong Nurseries, Ontario, Calif.				
H. Rockhill, Conrad, Iowa.	3 being propagated.		Latham × Older	Purple, hardy, firm.
H. M. Butterfield, Berkeley, Calif.				
A. C. Dike, Bristol, Vt.	Dike	1933	June × Latham	Heavy bearer, resistant to mosaic.
Canada:				
C. P. Newman, Ville La Salle, Quebec.	Newman	1919	From mixed seed of Herbert, King, Loudon, Cuthbert, and Eaton.	Hardy, productive, firm, mosaic-resistant.
	Newman 20	1915	Seedling of Eaton	Large, late, firm.
George Adams, Smithville, Ontario.	Adams 87			Hardy, bright red, does not turn dark.
	Adams 101			Firm, propagates by tip-rooting.
England:				
Laxton Bros., Bedford.	Bountiful	1917		Large, sweet.
	Prolific	1922		Productive.
	Renown	1925	Abundance × Superlative.	Bright, red, sweet.
	Yellow Hammer	1925		
	Reward	1935		
George Pyne, Topham, Devon.	Devon	1904	Seedling	Vigorous, large clusters; does not turn dark.
	Pynes Royal	1913	Seedling raised in 1907	Largest English, sweet.
	Red Cross	1917	Seedling	Tart, large, early.
	Park Lane	1922	do	High flavor.
	Mayfair	1929	Seedling of Park Lane	Do.
	Better-Late	1931	Blackberry-raspberry × raspberry.	Jam variety, very late.
	Imperial	1935	Seedling of Royal	Larger than Royal, conical, very vigorous, productive.

Source of Superior Qualities in Raspberries

Plant Characters

Hardy against cold. Ohta, Latham, Chief, Potomac (purple), Sarah, Starlight, Sunbeam, Newman, Adams 87, Newburgh, King, London, N. Y. 3024 (June × Brighton), P 117 (Latham × Farmer F_2 of North Dakota), Heath (black), Tekhas (in Russia).

Resistant to heat. Van Fleet, Dixie, Ranere.

Resistant to drought. Sodus, Latham, Marcy.

Resistant to leaf spot. Van Fleet, Ranere, U. S. D. A. No. 9 (Latham × Ranere), Dixie, Potomac, Evans; Pynes Royal and Baths Perfection (in England); *Rubus biflorus*, *R. innominatus*, *R. inopertus*, *R. kuntzeanus*, *R. parvifolius*, *R. phoenicolasius*.

Resistant to anthracnose. Van Fleet, *Rubus coreanus*, *R. kuntzeanus*, *R. biflorus*, *R. innominatus*, *R. niveus*, North Carolina R–14, Quillen and Naples (black), Potomac (purple), Ranere.

Resistant to yellow rust (*Phragmidium rubi-idaei*). Black raspberries (*Rubus occidentalis* and *R. leucodermis*) immune; highly resistant reds are Lloyd George, Owasco, Seneca, Antwerp, Ranere (not in California), Cayuga, Herbert, Chief.

Resistant to leaf rust (late raspberry rust). Hailsham red; all black raspberries are very resistant.

Resistant to spur blight. Columbian, Newman, and Marcy red show some resistance; probably all black varieties are resistant.

Resistant to streak. Potomac and all red varieties.

Immune to leaf curl. All purples and Farmer and New Logan blacks.

Resistant to green mottled mosaic. Latham, Chief, Ranere.

Escaping green mottled mosaic. Lloyd George, Herbert, Newman, Marcy, Indian Summer, Ranere, Potomac.

Resistant to mosaic in England. MacLaren, Baumforth A, Red Antwerp B.

Resistant to crown gall. Surprise (of California).

Resistant to verticillium wilt. Syracuse, Cuthbert, Ohta, Antwerp, Marlboro, Cayuga, Owasco, Seneca; Superlative and Black Antwerp A (in Europe); *Rubus biflorus*.

Resistant to aphid (*Amphorophora rubi*). Lloyd George, Herbert, Newburgh, Newman.

Everbearing. Ranere, La France, Erskin Park (summer bearing), Lloyd George (fall fruiting in the Northwest), Indian Summer, Hailsham (in England), November Abundance.

Fruit Characters

Early ripening. U. S. D. A. No. 0 (Latham × Ranere), Ranere, June, Chief Ohta, Marlboro, N. Y. 3024, Red Cross (in England); black varieties, Shuttleworth, Kansas, Bristol, Evans.

Late ripening. Van Fleet, Latham, Newman, Taylor, Cuthbert, N. Y. 3041; black variety, Rachel.

Firm. Potomac, Newman, U. S. D. A. No. 9 (Latham × Ranere), Newburgh, Latham, Ranere (in California); Baumforth seedling B, Burnett Holm, Penville Champion, and Pynes Royal (in England).

Large. Imperial, Pynes Royal, Lloyd George, Preussen (in England); Marcy, Newburgh, Taylor, Latham; Sodus (purple); Bristol, Dundee, and Cumberland (black).

Preserving. Cuthbert, Potomac, Columbian, Lloyd George.

Canning. Washington No. 89 (Cuthbert × Lloyd George); Cuthbert, Potomac, Royal, Sodus (purple).

Freezing. Latham, Chief, Viking (in the East); Washington No. 16, Lloyd George, Cuthbert, Viking, and Newburgh (in the West).

Small seed. Van Fleet, Lloyd George.

Bright red. U. S. D. A. No. 9 (Latham × Ranere), Washington No. 76 (Lloyd George × Cuthbert), Ohta, Ranere, Chief, June, Newman, Taylor, Adams 87, and Latham; Newburgh (in Oregon); Preussen (in England).

Do not turn dark. U. S. D. A. No. 9. Newburgh, Taylor, Viking, June, Adams 87; in England, Burnett Holm, Northward, Preussen, Baumforth B, Hornet A.

Excellent flavor. Cuthbert, Viking, Cayuga, Chief, Taylor; black varieties, Bristol, Evans, Honeysweet, Cumberland; in England, Norwich Wonder A, Preussen, Baumforth B, Hornet A, Pyres Royal, Park Lane.

Productiveness. Latham, Viking, Newburgh, June, Taylor, Marcy, and Bristol (reds); Cumberland (black); Potomac and Sodus (purple); in England, Lloyd George and Baumforth A.

Somatic Chromosome Numbers in Rubus

[See literature citations 7, 12, 22, 28, 29, 32, 35, 36, 37 An asterisk (*) after a name indicates an unpublished record of A. E. Longley]

14 somatic chromosomes

Blackberries:
- European:
  - *R. rusticanus* E. Merc.
  - *R. rusticanus inermis* Willd.
  - *R. tomentosus* Borkh.
  - *R. ulmifolius* Schott.
  - Burbank Thornless (*R. inermis* Willd.).
- American:
  - *R. allegheniensis* Porter.*
  - *R. argutus* Link.
  - *R. canadensis* L.
  - *R. setosus* Bigel.
  - Ancient Briton.*
  - Crystal White.*
  - Eureka (*R. cuneifolia* Pursh).*
  - Haupt.*
  - Jordan.*
  - Maxwell.*
  - McDonald.*
  - Pink.*

Raspberries:
- *R. adenophorus* Rolfe.
- *R. coreanus* Miq.
- *R. idaeus* L. (European red).
- *R. illecebrosus* Focke (strawberry-raspberry).
- *R. kuntzeanus* Hemsl.
- *R. lasiostylus* Focke.
- *R. leucodermis* Dougl. (western black-cap).
- *R. mesogaeus* Focke.
- *R. occidentalis* L. (eastern blackcap).
- *R. odoratus* L. (eastern flowering raspberry).
- *R. parviflorus* Nutt. (western flowering raspberry).
- *R. phoenicolasius* Maxim. (wineberry).
- *R. spectabilis* Pursh (salmonberry).
- *R. strigosus* Michx. (American red raspberry).
- *R. triphyllus* Thunb.
- *R. xanthocarpus* Bur. and Franch.
- Cardinal (purple).
- Cumberland (black).
- Cuthbert (red).
- Eaton (red).
- Gregg (black).
- King (red).
- Lloyd George (European red).
- Newman (red).
- Queen Alexandra.

14 somatic chromosomes—Continued

Raspberries—Continued.
- Ranere (red).
- Royal (purple).
- Superlative (European red).

21 somatic chromosomes

Blackberries (American):
- Marvel (Florida Marvel).
- 13 wild forms of New England, probably hybrids.
- 12 wild forms of Maryland and District of Columbia, also probably hybrids.*

Raspberries:
- All Summer.
- Belle de Fontenay.
- Erskine.
- Merveille Rouge.
- November Abundance.
- White Queen.

Blackberry-raspberry hybrids:
- Kings Acre.*
- Mahdi.

28 somatic chromosomes

Blackberries:
- European:
  - *R. acuminatus* Lindeb.
  - *R. affinis* Weihe and Nees.
  - *R. arrhenii* J. Lange.
  - *R. bloxamii* Lees.
  - *R. caesius* L.
  - *R. calvatus* Blox.
  - *R. cletrophilus* P. J. Muell.
  - *R. corylifolius* Sm.*
  - *R. genevieri* P. J. Muell.
  - *R. hirtus* Waldst. and Kit.
  - *R. imbricatus* Hort.
  - *R. incurvatus* Bab.
  - *R. insularis* Aresch.
  - *R. kaltenbachii* Metsch.
  - *R. lindleyanus* Lees.
  - *R. nemorosus* Arrh.
  - *R. nitidioides* Watson.
  - *R. nitidus* subsp. *opacus* Focke.
  - *R. pallidus* Weihe and Nees.
  - *R. plicatus* Weihe and Nees.
  - *R. polyanthemus* Lindeb.
  - *R. radula* Weihe.
  - *R. radula* var. *angustifolia* Lund.
  - *R. schlechtendalii* Weihe.
  - *R. sprengelii* Weihe.

28 somatic chromosomes—Continued

- Blackberries—Continued.
  - European—Continued.
    - *R. strivultus* f. Kullensis.
    - *R. suberectus* G. Anders.
    - *R. thyrsiger* Banning and Focke.
    - *R. villicaulis* Koehl.
    - Edward Langley.
    - Evergreen or Cut-Leafed.
    - Himalaya (*R. procerus* P. J. Muell.).
    - John Innes.
    - Pollard.*
    - Sherlock Jr.*
  - American:
    - Two wild forms of Maryland, probably hybrids.*
    - Badger.*
    - Brainerd.
    - Early Wonder.*
    - Eldorado.*
    - Johnson.*
    - Joy.*
    - Jumbo.*
    - La Grange.*
    - Lawton.*
    - Mersereau.*
    - Miller.*
    - Nanticoke (*R. cuneifolius* Pursh).*
    - Queen.*
    - Snyder.*
    - Taylor.*
    - Texas Everbearing.*
    - Ward.*
- Raspberries:
  - Hailsham.
  - La France.
  - Merveille Rouge.
  - Merveille de Quatre Saisons.
  - Surpasse Merveille à blanc.
- Blackberry-raspberry hybrid:
  - Veitchberry.

35 somatic chromosomes

- Blackberries:
  - European:
    - *R. bellardi* Weihe and Nees.
  - American:
    - Two wild forms of Maryland, probably hybrids.*
    - Two wild forms of New England, probably hybrids.*
    - Logan seedling.
    - Logan × Mammoth seedling.

42 somatic chromosomes

- Blackberries:
  - European:
    - *R. borreri* Bell Salt.
    - *R. ciliatus* Lindeb.
    - *R. divergens* Neum.
    - "*R. insulariformis*"-*R. wahlbergii* Arrh.
    - *R. nitens* Lindeb.
    - *R. tiliaceus* Liebm.
    - Bedford Giant.
  - American:
    - Five wild forms of New England, probably hybrids.
    - *R. loganobaccus* Bailey.
    - Logan (Loganberry).
    - Cory.*
    - Erie.*
    - Lucretia.
    - Mammoth.
    - Phenomenal.
    - Rathbun.

45 somatic chromosomes

- Blackberries (European):
  - *R. eluxatus* var. *subnitidus* Lidf.

49 somatic chromosomes

- Hybrid blackberries (European):
  - Laxtonberry.
  - *R. lagerbergii* Lindeb. var. *balticus* Aresch.

56 somatic chromosomes

- Dewberries (American):
  - One wild form of Massachusetts.
  - Austin Thornless.
  - Ideal Wild.
  - Premo.*
  - Windom.*
  - Form close to *R. loganobaccus* Bailey.

70 somatic chromosomes

Form close to *R. loganobaccus* Bailey.

84 somatic chromosomes

R. macropetalus Dougl., of Oregon and Washington.

IMPROVEMENT OF CURRANTS AND GOOSEBERRIES

GEORGE M. DARROW, Senior Pomologist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry

CURRANTS and gooseberries are closely related bush fruits that are far more extensively raised and prized in Europe than in the United States. They were formerly grouped into a single genus, *Ribes*, but now the gooseberries are generally placed in a separate genus, *Grossularia*. Though hybrids have been made between currants and gooseberries, only sterile seedlings have so far been raised.

MATERIAL FOR CURRANT BREEDING

THE red currant seems to have been cultivated first some time before 1600 in the Netherlands, Denmark, and around the Baltic Sea. According to Hedrick,[1] in 1665 Rea mentioned three red currant varieties, one white, and one small black. Currant bushes were ordered for the Massachusetts colony in 1629; thus they were early brought to North America. By 1826 about 20 cultivated varieties were known in England, a good many of which were brought to the United States soon after their introduction. Most of the currant industry was based on European varieties until about 1890. Fay, a seedling raised by L. Fay, Portland, N. Y., in 1868, was introduced in 1880; Wilder, a seedling of Versailles, was raised by E. Y. Teas, Irvington, Ind., about 1877; Red Cross and Diploma both originated from a cross between Cherry and White Grape made in 1885 by J. Moore, Attica, N. Y.; and Perfection originated in 1887 from a cross of Fay × White Grape made by C. G. Hooker, Rochester, N. Y. These five varieties quickly became important and constitute possibly 85 percent of the total present acreage. London Market and Victoria, the other principal varieties, are old European sorts. Thus the currant industry in the United States is based largely on varieties originated by American breeders.

The European black currant is extensively cultivated in Europe and to a lesser extent in Canada, but it has been found to be by far the most susceptible host for the white-pine blister rust fungus, and the United States Department of Agriculture advises against its cultivation in States where white pines are important forest trees.

The American black currant (fig. 1) is a much less susceptible alternate host for the blister rust fungus than the European black currant. Though cultivated as a garden crop, there is probably very little commercial acreage of this fruit. The best-known variety is the

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[1] HEDRICK, U. P., assisted by HOWE, G. H., TAYLOR, O. M., BERGER, A., SLATE, G. L., and EINSET, O. THE SMALL FRUITS OF NEW YORK. 614 pp., illus. Albany. (N. Y. (State) Dept. Farms and Markets Ann. Rept. (1924-25) 33, pt. 2.)

Crandall, which has large berries. It grows well in the prairie regions with hot summers, but its berries ripen so unevenly that they must be picked singly. N. E. Hansen selected and introduced four American black varieties—the Tonah, Atta, Mato, and Wanka—in 1925. These bear fruit of larger size than the ordinary wild black currant.

In 1923 Thayer's work on the red and the white currant was published.[2] This aided greatly in identifying varieties and classifying

Figure 1.—The American golden or black currant. An extremely hardy and drought-resistant native currant that is a much less receptive host of the white-pine blister rust than the European black currant.

them as to their botanical origin. In 1924 Berger[3] covered species and varieties of both currants and gooseberries, and his work is very helpful in studying the group. Hedrick and his associates[4] also described the species and varieties and gave colored plates of many of the more important types.

Relation of Currants and Gooseberries to White-Pine Blister Rust

After the white-pine blister rust epidemic had shown this disease to be a serious menace to white pines in the United States, eradication of currants and gooseberries, the alternate hosts of the blister rust

[2] Thayer, P. The red and white currants. Ohio Agr. Expt Sta. Bull 371, pp 307-394, illus. 1923.
[3] Berger, A. A taxonomic review of currants and gooseberries. N. Y. Agr. Expt Sta. Tech. Bull. 109, 118 pp., illus. 1924.
[4] Hedrick, U. P., assisted by Howe, G. H., Taylor, O. M., Berger, A., Slate, G L , and Einset, O. See footnote 1.

fungus, was undertaken in sections where the white pine is important. This has restricted interest in both currants and gooseberries, and in large areas, as in New England, most of the cultivated currants and gooseberries have been eradicated. As a consequence, the acreage of currants in the United States reported for 1929 by the 1930 census, 3,574 acres, was less than half of the 7,379 acres reported in 1919. Only 1,302 acres of gooseberries were reported in 1929.

The white-pine blister rust was brought into the United States between 1898 and 1910 on white-pine planting stock imported from Europe. It is now established throughout most white-pine regions of the United States from Maine to Virginia, west to Minnesota, and in Montana, Idaho, Oregon, and Washington. Recently it has been found in northwestern California. It injures all species of the white-pine group (five-needle pines), which are among the most valuable timber trees of the northern United States, having an estimated stumpage value of about $400,000,000. The disease cannot spread from pine to pine, but only from pine to currant and gooseberry and then from these back to pine. It causes a rust on the leaves of currant and gooseberry, which may defoliate the most susceptible varieties.

Valuable white-pine forests can be protected by eradicating wild and cultivated gooseberries and currants for a distance of about 900 feet around white pines, except that black currants must be destroyed for greater distances from pines.

Currants and gooseberries differ greatly in their susceptibility to the white pine blister rust. As already noted, the common cultivated black currant—the European black currant (*Ribes nigrum* L.)—because of its high susceptibility has been the chief agency in the rapid and long-distance spread of the disease throughout the Northern States. The American black currant (*R. americanum* Mill.), the golden currants (*R. odoratum* Wendl. and *R. aureum* Pursh), and the native gooseberries (*Grossularia divaricata* (Dougl.) Spach and *G. curvata* (Small) Cov. and Britton) have seemed somewhat more sus-

AMERICAN *native species of gooseberries range from Florida far north into Canada, and some of them are resistant to high summer temperatures and to the leaf diseases that have discouraged gooseberry growing in this country. By suitable crossing, these characteristics can be combined with the great size, the fine flavor, and the beauty of varieties developed in Europe through generations of breeding, encouraged by a public that had a great fondness for this fruit. Some of the hybrids already produced in this country show what can be done in the way of improved quality and size of fruit and vigor of plant. There is no doubt that the gooseberry offers opportunities for the development of improved varieties that would be welcome additions to our gardens.*

ceptible than most cultivated varieties. Franco-German, Netherlands, and London Market currants are very resistant or nearly immune, while cultivated varieties of gooseberries are very resistant.

To protect white-pine stands, many States have established regulations governing the planting of currants and gooseberries, and some for white pines. In general, currant and gooseberry plantings are prohibited where white pine is important, and white-pine plantings where the currants and gooseberries are important. Before planting these fruits the State laws should be consulted. Summaries of the laws are given in Farmers' Bulletin 1398.[5]

G. G. Hahn, of the Division of Forest Pathology, Bureau of Plant Industry, has recently tested the Viking red currant, a variety introduced from Norway, and found it immune to blister rust. Propagating stock has been imported, and in 1935 and 1936 a large number of plants were distributed to experiment stations for testing as to its horticultural value and for breeding. Plants already fruiting in New England and New York have shown that it is of good dessert quality and desirable for jelly making. A few open-pollinated Viking seedlings, produced where cross-pollination was not eliminated, have been slightly susceptible to blister rust. The culture of the Viking in white-pine areas will depend on the policy within each State after its horticultural value and seedling susceptibility to the fungus have been fully determined.

SPECIES OF CURRANTS

Berger states that there are about 150 species of currants and gooseberries distributed all over the Northern Hemisphere, but mostly in North America, and extending along the mountains of the Americas as far south as Patagonia. At least 100 species are currants and some 50 are gooseberries. The Rocky Mountains in North America are especially rich in species. There are about 15 species of red currants, of which *Ribes sativum* Reichenb., *R. rubrum* L., *R. warscewiczii* Jancz., and *R. petraeum* Wulfen, and hybrids of them are considered important for breeders.

Ribes sativum.— A native of western Europe, frequently escaped from cultivation in North America. Leaves heart-shaped at base, five-lobed and with lobes spreading to the side, clusters 10- 20-flowered, flowers flat, greenish yellow. Chautauqua, Diploma, Red Cross, Versailles, and Wilder are typical varieties, while Cherry and Fay belong to a section of the species.

Ribes rubrum.—Northern Europe to northern east Asia. This species is more northern than *R. sativum*, from which it is most easily distinguished by its forward-pointing leaves and cup-shaped flowers. Leaves truncate or subcordate at base and lobes cupped or pointing forward, broader than long, clusters longer, flowers cup-shaped, pale green or brownish. London Market and Victoria are typical varieties. Perfection is derived from *R. rubrum* × *R. sativum*.

Ribes warscewiczii.—A very productive species of eastern Siberia, worthy of use in breeding. Leaves large, heart-shaped; clusters about 15-flowered, flowers coppery red to pale flesh-colored; fruit large, blackish purple, very acid. Near to *R. rubrum*, but flowers larger and fruit more acid.

Ribes petraeum.—Very widely distributed over Europe, northwestern Africa, and northern Asia. Leaves roundish, pubescent when young; flowers bell-shaped, green streaked with red or purple; fruit red or blackish red, more acid than *R. sativum* or *R. rubrum*. Growth starts late in spring. Prince Albert is derived from *R. petraeum* × *R. rubrum*, and Gondouin from *R. petraeum* × *R. sativum*.

[5] DARROW, G. M., and DETWILER, S. B. CURRANTS AND GOOSEBERRIES; THEIR CULTURE AND RELATION TO WHITE-PINE BLISTER RUST. U. S. Dept. Agr. Farmers' Bull. 1398, 38 pp., illus. 1924.

The black currants of Europe are all derived from *Ribes nigrum*. It is more vigorous than the red currant species, and the whole plant has a characteristic aroma. To many the fruit flavor is objectionable; to others highly pleasing. It is a native of Europe as far north as Scandinavia, and of northern and central Asia. An allied species, *R. ussuriense* Janc , is native to eastern Manchuria, but the plant has a camphorous aroma and the fruit has no odor. The American black currant, *R. americanum*, has an aroma in the plant and fruit similar to that of *R. nigrum*. It ranges from New Mexico to Virginia northward into Canada. One variety, Sweet Fruited Missouri, has been in cultivation, though the fruit is sometimes gathered in the wild. It is not especially promising.

The golden currants, native in central and northwestern United States to northern Mexico, are often known as American black currants Yellow- or golden-fruited forms are common. The most common variety is the Crandall, with rather large fruit. There are several species, but all are close to *Ribes odoratum*, to which the Crandall belongs.

There are many ornamental species of currants in the Rocky Mountain region, but they are mostly of little value for their fruit.

MATERIAL FOR GOOSEBERRY BREEDING

THE gooseberry seems to have come into cultivation at about the same time as the currant. According to Hedrick, it was grown in English gardens before 1600. By 1629 there were 3 red varieties, a blue, and a green variety described; by 1778, 24 varieties were described; by 1825, 185 kinds were listed; and in 1831 a list of 722 varieties was published. The great development in the size of the European gooseberry was in part due to the high esteem in which it is held in England, and to the shows held there. For example, 171 gooseberry shows were held in England in 1845. Prizes were given for the heaviest fruits, and in 1852 a berry of the London variety was shown that weighed 7 grams (about one-fourth ounce), or seven to eight times the weight of the wild fruit.

In North America the European gooseberries were attacked by mildew, and gooseberries were little grown until after the Houghton was originated from seed planted in 1833 by A. Houghton, Lynn, Mass. Houghton was from a cross of the European with an American variety, and from seed of it Charles Downing, Newburgh, N. Y., raised the Downing about 1855 (fig. 2, *C*). The gooseberry industry of the United States was largely based on these two varieties until about 1900, or until after the use of fungicides became common so that mildew could be controlled on varieties from Europe or of European parentage, such as Chautauqua and Industry. Since 1900 several varieties have become prominent: Oregon (Oregon Champion), a cross between Crown Bob and Houghton, raised about 1860 by P. Prettyman in Oregon; Pearl, a cross of Downing × Red Warrington, originated by William Saunders, London, Ontario, and introduced in 1888; Red Jacket (Houghton × Red Warrington), also originated by Saunders and introduced about 1890; Carrie, a seedling of Houghton, raised by W. Elliot, Minneapolis, Minn., and introduced in 1905;

Poorman, a seedling raised by W. H. Craighead, Brigham, Utah, and introduced in 1896; and Como (Pearl × Columbus), originated at the Minnesota Agricultural Experiment Station and introduced in 1922. Of these varieties, Poorman (fig. 2, *B*) has the best appearance and

Figure 2.—*A*, Columbus, a large European gooseberry; *B*, Poorman gooseberry, the largest of the hybrids between American and European varieties; *C*, Downing, a hybrid that has long been the most important American gooseberry.

is excellent in quality, comparing favorably with the best European sorts. Though considered a cross between Downing and Houghton, it may possibly have been a cross with one of the Rocky Mountain species.

Species of Gooseberries

The gooseberries of Europe are derived from the one species *Grossularia reclinata* (L.) Mill., which ranges from northern Africa through Europe from Spain to the Caucasus, north to Scandinavia. *G. uva-crispa* (L.) Mill., a native of central Europe, is said to be more drought-resistant, with very sweet late fruits. It starts growth about 2 weeks later than the species. Berger considers that the Houghton was derived from a cross of this form of the European gooseberry with *G. hirtella*. Most of the rest of the species of gooseberries are natives of North America, and several are promising for breeders.

Grossularia cynosbati (L.) Mill.—Native from North Carolina to Missouri, north to Manitoba and New Brunswick, Berry prickly, wine red, with a rather thick skin. Bush to 4.5 feet high; common in woods and rocky places.

Grossularia missouriensis (Nutt.) Cov. and Britton.—Native from Tennessee to Kansas, north to Minnesota and South Dakota. Berry not prickly, purplish. Bush to 6 feet high. The Glenndale, derived from this crossed with European varieties, is very vigorous and productive and stands the hot summers better than other gooseberries.

Grossularia divaricata (Dougl.) Spach, the coast gooseberry.—Native from central California to British Columbia. Berry small, dark purple or black, not prickly. Bush 6 to 10 feet. Trebla, a variety propagated by A. F. Etter, is supposed to have been derived from a cross of this species with cultivated varieties.

Grossularia hirtella (Michx.) Spach.—Native from West Virginia to South Dakota and north to Newfoundland and Manitoba. Berry purple or black, not prickly. Bush to 3.5 feet. Houghton, Downing, Pearl, Carrie, Oregon, and other varieties are considered to have been derived from crosses of this species with the European varieties. It has given mildew resistance to American varieties.

Grossularia oxycanthoides (L.) Mill.—Native from Michigan to North Dakota, north to Newfoundland and the Yukon. Berry smooth, purple, sweet, good; bush low, spreading; branches bristly. A hardy, far-northern species.

Grossularia nivea (Lindl.) Spach, the Snake River gooseberry.—Native to northern Nevada, Idaho, eastern Washington, and Oregon. Berries smooth, bluish black, very good; bush 5 to 10 feet high; somewhat similar to *G. missouriensis*.

Grossularia curvata (Small) Cov. and Britton.—Native from Georgia to Texas. Berry green to purplish, smooth; bush low, spreading; branches arching. Promising for breeding, because native to the South.

Grossularia echinella Cov.—Native to northern Florida. Berry very prickly, large, green, bush spreading. Promising for breeding because native to the South and because of its large fruits.

Grossularia rotundifolia (Michx.) Cov. and Britton.—Native from North Carolina to Massachusetts in rocky places in woods. Berries smooth, purplish; bush with slender arching branches.

Grossularia irrigua (Dougl.) Cov. and Britton, the inland black gooseberry.—Native to western Montana and eastern Oregon, north to British Columbia. Berries smooth, purple or black; bush 3 to 10 feet high.

Besides these species there are others in the western United States that may be of value. Thus *Grossularia lobbii* (A. Gray) Cov. and Britton, *G. pinetorum* (Greene) Cov. and Britton, *G. sericea* (Eastwood) Cov. and Britton, and *G. marshallii* (Greene) Cov. and Britton have large fruits but with prickles or glandular bristles. Of the species listed above, *G. nivea* is possibly one of the most promising for breeding.

SYSTEMATIC BREEDING WORK WITH CURRANTS AND GOOSEBERRIES

Very little systematic breeding work has been done with currants and gooseberries. The fact that nearly all the red currant varieties grown in this country originated here indicates the possibilities for

improvement of this fruit, particularly in breeding for resistance to leaf diseases; and this is borne out by the more recent red currant work at the Minnesota Agricultural Experiment Station. Varieties of red currants resistant to cane blight (*Botryosphaeria ribis* Gross. and Dug.) and with foliage resistant to leaf spot (*Septoria ribis* Desm.) are needed to make the currant a useful garden and commercial fruit in many sections where it is now difficult to grow. The hardiness, drought resistance, and great vigor of the American black currants (golden currants) make this group also promising. Selections of these currants are needed that mature many or all berries on a cluster, so as to reduce the cost of harvesting.

Probably the greatest opportunity, however, is in gooseberry breeding. The chief need is for fine-flavored, attractive-fruited varieties that are resistant to leaf spot, to high summer temperatures, and to mildew (*Sphaerotheca mors-uvae* (Schw.) Berk. and Curt.). Such southern native species as *Grossularia echinella* and *G. curvata* endure high summer temperatures and are resistant to mildew. Some resistance to leaf spot seems to be shown by *G. missouriensis* and probably certain other native species. European gooseberries cross readily with American species, and the productiveness and vigor of the hybrids have indicated how promising this line of work might be. Poorman, though not so large as many of the European gooseberries, is larger than the other hybrids and has greater beauty and better flavor when ripe than European varieties now grown in this country. The Glenndale has greater vigor than most other hybrids and far greater vigor than the European sorts. American native species range from Florida far north into Canada; and varieties with the size of the European, the quality and beauty of Poorman, the vigor of Glenndale, and the range of American species would be welcome additions to our garden fruits.

Work of Experiment Stations With Currants and Gooseberries[6]

In South Dakota, crosses were made between the native wild gooseberry of South Dakota (*Grossularia missouriensis* (Nutt.) Cov. and Britton) and the large-fruited European varieties. The first hybrid variety to be introduced was Sunset in 1924, followed in 1925 by Kabu, Kaduza, Kana, Kanga, Kapoza, Kataga, Kawauka, Kazouta, Kaza, and Kopa. In addition, the station has grown many thousands of seedlings of the native gooseberry, selecting the best for a new generation. Seedlings of the native wild gooseberry were first introduced in 1921, and up to 1927 eight generations of seedlings had been raised.

Similar work in growing thousands of seedlings of the wild black currant resulted in the selection in 1923 of large-fruited seedlings. Four were named and introduced in 1925—Tonah, Atta, Mato, and Wanka. In addition the Siberian black currant, collected by Hansen in 1897 in Siberia, was introduced in 1910.

In North Dakota, breeding with the gooseberry was begun in 1920, the native wild gooseberry (*Grossularia missouriensis*) being crossed

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[6] A. S. Colby (Illinois), G. L. Slate (New York), A. N. Wilcox (Minnesota), and A. F. Yeager (South Dakota) kindly furnished details of the breeding work with currants and gooseberries at their experiment stations.

with Oregon Champion, Transparent, Houghton, Downing, Copland, Josselyn, and Carrie. The best combination was with the Oregon Champion. In 1932 three of the seedlings were named and introduced—the Pixwell, Abundance, and Perry. Pixwell is considered especially good for jelly, preserves, and sauce. *G. setosa* Lindl., another wild gooseberry from North Dakota, was also crossed with Oregon Champion, and though the first hybrid generation was not particularly promising, the second showed better seedlings. A. F. Yeager, in charge, noted that red color of fruit was dominant over green, smooth fruit over downy, and long pedicel and peduncle over short. He also found a dwarf plant type in Oregon Champion crosses and observed that a light-green color of unripe fruit was apparently, dominant over dark-green color. He is studying inheritance of thorns, winter hardiness, and drought and heat resistance.

In New York gooseberry breeding was begun at the New York (State) Agricultural Experiment Station at Geneva in 1892 and has been continued at intervals since. The Fredonia, introduced in 1926, is the only variety resulting from the work. It is a seedling of Crown Bob and is large, late, and productive for an English type. Among the varieties crossed are America, Boskoop, Black Champion, Chautauqua, Crandall, Downing, Honing Fruheste, High Sheriff, Houghton, May Duke, Lancashire Lad, Pale Red, Wellington Glory, Whitesmith, and Victoria. This station maintains a very large collection of species and varieties.

A small number of currant crosses have been made, but no varieties have been introduced. A large collection of currant varieties and species is also maintained. George L. Slate reported that crosses have been made as follows:

Fay × Missouri Sweet Fruited.
Fay × Crandall.
White Transparent × Crandall.
Cherry × Crandall.
Black Naples × White Transparent.
White Transparent × Black Naples.
Diploma × Black Naples.
Lee (black) × Mountain (gooseberry).
Black Naples × Downing.
Boskoop (black) × Poorman.
Lee × Poorman.
Boskoop × *Ribes sanguineum.*
Chautauqua × *Grossularia echinella.*
R. nigrum L. × Ozonne.
Honing Fruheste × *R. pinetorum.*
Honing Fruheste × *R. lacustre.* (?)
May Duke × *R. pinetorum.*
May Duke × *R. lacustre.*
R. pinetorum × *R. lacustre.*
R. pinetorum × *R. odoratum.*
R. pinetorum × *R. innominatum.*
R. lacustre (?) × *R. pinetorum.*

In Minnesota the breeding of gooseberries was begun in 1909 and has been continued since. Carrie, Chautauqua, Columbus (fig. 2, *A*), Houghton, Josselyn, and Pearl have been intercrossed and crossed with selections of wild species. *Ribes hirtella* Spach has been used to obtain thornlessness. Como, a cross of Pearl × Columbus, was introduced in 1922. It has resistance to sun scald and to disease and is productive. It is especially good in cooking qualities.

The raising of seedling currants was begun in 1912 and has been continued to the present. No crossing has been done. The Red Lake variety was introduced in 1933, being selected for the large size of the berry and of the cluster and for its productiveness. It is succeeding well in New Jersey and in other Eastern States.

In Illinois the work with gooseberries was begun in 1924 with the objective of obtaining greater production, larger size, higher flavor,

fewer thorns, and disease-resistant foliage. Poorman, Spinefree, Chautauqua, Carrie, Glenndale, and Transparent have been intercrossed, and over 2,000 seedlings are under test. Papers by Colby,[7] in charge, indicate the accomplishments.

Work of the United States Department of Agriculture with Currants and Gooseberries

The work at the United States Northern Great Plains Field Station at Mandan, N. Dak., under W. P. Baird, has consisted largely in raising seedlings and making selections of the native hardy, drought-resistant, productive wild black currant *Ribes odoratum*. In 1924, selections of this currant were crossed, and about 50 selections have been made. Baird has noted that black fruit is dominant over yellow and red and that a round shape is dominant over oblong. Some gooseberry and red currant breeding has been done. The drought of 1936 killed most of the gooseberry and red currant selections, but the black currants withstood it.

At Corvallis, Oreg., a collection of the best-fruited forms of the native species of currants and gooseberries was made by L. N. Goodding, and hybridizing was begun by George F. Waldo.

At Washington, D. C., crosses have been made in recent years by F. V. Coville and O. M. Freeman between *Grossularia echinella*, a gooseberry species native to Florida, and cultivated varieties. Several selections were made, and the second hybrid generation is being raised at Beltsville, Md.

In 1932 the Glenndale gooseberry was introduced. This originated as a seedling raised by the late W. Van Fleet probably about 1905, before he joined the Department of Agriculture, from a cross of ((*G. missouriensis* × Red Warrington) × Triumph) × Keepsake. It is a very rank-growing variety, which succeeds from Maryland and Virginia to Kansas, at the southern limit of gooseberry growing.

Currant and Gooseberry Breeding in Foreign Countries

The Dominion station at Ottawa, Canada, has introduced at least four varieties of gooseberries—Charles, Silvia, Mabel, and Spinefree, the last-named being a cross of a second-generation thornless wild with Mabel. It is described as of good flavor, thick-skinned, bright red, free of spines, upright, vigorous, free of mildew, and resistant to leaf spot.

This station also introduced the following 12 black currants originated by William Saunders before he became director in 1887: Climax, Clipper, Eclipse, Ethel, Kerry, Magnus, Ogden, Ontario, Saunders, Success, Topsy, and Winona. Of these, Kerry, Clipper, Eclipse, and Climax are recommended varieties in Canada.

At the East Malling Horticultural Research Station in England, the production of improved varieties of red and black currants is a breeding project. The use of X-rays to induce mutations, and a study of inheritance in black currants, are two lines of research now under way.

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[7]Colby, A. S. SIZE INHERITANCE IN GOOSEBERRY FRUITS. Amer. Soc. Hort. Sci Proc. (1933) 30: 105-107. 1934.

——— INHERITANCE OF GOOSEBERRY LEAF INFECTION. Amer. Soc. Hort. Sci. Proc. (1934) 32: 397-399. 1935.

At the University of Bristol production of heavy-cropping varieties of black currants is one objective, and two varieties have been named and introduced. At times some gooseberry breeding for mildew resistance has been carried on at this station.

Laxton Bros., of Bedford, England, have done much breeding work with black currants and gooseberries, and some with red currants. They have introduced the following red currants and gooseberries:

TABLE 1.—*Currants and gooseberries introduced by Laxton Bros., of England*

Variety	Year introduced	Parentage	Superior qualities
Red currants			
Perfection	1909		Long clusters, sweet, large
Laxton's No. 1	1925		Vigorous, productive
Gooseberries			
Bedford Yellow	1915	Gold Drop × Drill	Golden yellow, high flavor, large
Amber	1916	Wonderful × Lancaster Lad	Amber color, high flavor
Bedford Red	1922	Crown Bob × Langley Green	Red, productive
Green Gem	1922	Drill × Whitesmith	Yellowish green, high flavor
Emerald	1925	Drill × Crown Bob	Early, green, productive
Golden Ball	1928	Drill × Whitesmith	Yellow, high flavor
Rearguard	1928	Wonderful × Lancaster Lad	Very late, firm

In Sweden, C. G. Dahl, in charge of the gooseberry breeding at Alnarp, reported that breeding was begun in 1911 to obtain mildew-free varieties. *Grossularia divaricata* (Dougl.) Cov. and Britton and *G. nivea* (Lindl.) Spach were crossed with European varieties. Some 1,000 plants were raised, and one variety, Scania, has been introduced. It is free from mildew and produces a strong plant and large fruit. A second variety, a second-generation hybrid from *S. nivea* × a European variety, is being distributed under the name Centum. It is also free from mildew, with fruit like Downing, of fine flavor.

In the Union of Soviet Socialist Republics, I. V. Michurin originated one gooseberry variety, Shtambooii, which was reported to be resistant to mildew.

SOME UNUSUAL OPPORTUNITIES IN PLANT BREEDING

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OPPORTUNITIES for the development of new and improved plants by breeding are by no means limited to those now grown in home or commercial gardens. All our present cultivated plants, it must be remembered, have been derived from wild plants. Those that were most outstandingly useful or most readily adaptable to cultivation, man took from forest and field and grew in his own dooryard. Others he left in their wild state, for one reason or another, though he continued to use their products. One of the plants left wild until very recently was the blueberry. The work of the late Frederick V. Coville, described elsewhere in this Yearbook, shows how modern knowledge and modern technique, applied to suitable wild material, can change and improve it enormously for human uses. Not all neglected wild plants, undoubtedly, would produce such splendid results as the blueberry under Coville's handling, but the achievement suggests that there is a wealth of material not yet touched, awaiting merely the right imagination and the right opportunity for the breeder to transform it in greater or less degree.

Some of the native wild plants and introductions from foreign countries need only careful selection of superior strains to increase their usefulness. In other cases a planned program of breeding is necessary, including crosses with types already in cultivation. It must be recognized that hybrids between distinct species are made with considerable difficulty in most cases, and only rarely are they directly valuable in a horticultural way. However, occasionally valuable things do come from such distant crosses, and the only way to find them is to make the attempt.

PLANTS THAT AWAIT THE BREEDER'S ATTENTION

SOME of this material may be mentioned at random here. In the Northeastern States some people use milkweed like asparagus and also make soup of it. If varieties with many short internodes on their underground stems could be located and improved by breeding, they might be a welcome addition to the perennial vegetable garden. Different colored varieties of the butterfly milkweed might be selected and bred as ornamentals. Strains of the hard or sugar maple that came true to various autumn leaf colors would be desirable additions to our list of shade trees, and others might be found with unusually high sugar content in the sap, to be used in the sugar bush. Search

might reveal strains of longleaf pine trees having high turpentine yield. Trees of upright narrow form have special value in landscape use, especially for screens, high hedges, and narrow streets. Lombardy poplar, quite widely used for this purpose, usually proves short-lived. If more varieties of long-lived trees of this form could be developed, they would be valuable additions to our nursery products. Such forms have been propagated from American elm, several species of maple, English oak, oriental cherry, and others, but they have never been as extensively planted as this form warrants. Chinese elm apparently has received little attention from the standpoint of developing varieties of columnar or pyramidal or low-growing dense form, though such varieties would be useful, especially in sections subject to drought and other conditions adverse to some of the other trees.

Native hardy rhododendrons and azaleas are a fascinating group for breeding, with the object of developing varieties that would endure the summer heat encountered from Philadelphia southward better than present varieties, and also of increasing the winter-hardiness of some Asiatic forms, especially *Rhododendron obtusum* Planch. and allied species. Although this group of plants is rather limited in its adaptability because of soil and climatic requirements, its use is increasing very rapidly wherever any of its diverse forms can be grown well. *R. calendulaceum* Torr., the flame azalea of the southern Appalachians, owing to its hardiness and splendid range of colors, offers a good subject not only for crossing with other species but also for selecting the best specimens in the wild and propagating them as varieties.

There are many unusual or unimproved native and introduced fruits awaiting the attention of the breeder. Some of these have been studied more or less casually, but many are worthy of systematic continued study. For the Northern States there are the barberries (*Berberis* spp.); buffaloberries (*Shepherdia* spp.); cornelian-cherry (*Cornus mas* L.); elderberries (*Sambucus* spp.); hawthorns (*Crataegus* spp.); honeysuckles (*Lonicera* spp.); juneberries, known also as shadberries, shadblow, or sarvisberries (*Amelanchier* spp.); mulberries (*Morus* spp.); mountain ash (*Sorbus* spp.); wintergreen and salalberries. (*Gaultheria* spp.); and for the more southern States, elderberries, juneberries, the mayhaw (*Craetaegus aestivalis* Torr. and Gray), the species of *Eugenia*, feijoa (*Feijoa sellowiana* Berg.), the pawpaw (*Asimina triloba* L.), and the persimmon (*Diospyros virginiana* L.). The writers have been especially interested in the actinidias, the American cranberrybush, several species of *Elaeagnus*, the oriental quinces, and the Chinese bush cherries. Brief discussions of these as material for the plant breeder are given in the following pages. Some of the other fruits previously listed are just as promising, but they have not been so readily available to the writers.

ACTINIDIA

THE actinidias (known also as Chinese or Japanese gooseberries and sheep peaches) are climbing shrubs, chiefly of eastern Asia, ranging from the northern part of Japan south to the tropical islands.

Some seven species are in cultivation chiefly as ornamentals, for their beautiful foliage is remarkably free from insects and fungi. Two species, at least, are worth cultivating for their fruit, *Actinidia arguta* Miq., which is hardy in New England (fig. 1), and *A. chinensis* Planch., which is hardy north to Washington, D. C., though the growing season does not seem to be long enough at Washington to mature the fruit. In southern California very fine crops of *A. chinensis* are sometimes produced. The fruit of *A. arguta* is about an inch long, that of *A. chinensis* up to 2 inches, or about the size and shape of a medium to small hen's egg. The fruit is tart until fully ripe, when it is sweet, with a texture somewhat like that of a fresh ripe fig. It is used fresh, for jelly, and for sauce. The leaves of *A. chinensis* are relished by cats, like catnip. Michurin, the Russian plant breeder, has intro-

Figure 1.—One of the actinidias (*Actinidia arguta*) on a trellis at the Arnold Arboretum, Boston, Mass. The actinidias are potentially important food plants of the United States, just awaiting the study of a plant breeder. This species bears fruit about an inch long; but another kind, *A. chinensis*, bears fruit up to 2 inches long.

duced five varieties, Ananasia Michurin, Clara Zetkin, Pozdniaia (late), Raniaia (early), and Urezhainaia (high-yielding). The beauty of the vines, their wide climatic adaptation, their vigor, and the pleasing flavor of the fruit make them promising for the United States. They are readily propagated by softwood and hardwood cuttings and by layering. The one need is the origination of varieties regularly productive, for the seedlings now grown only rarely produce heavy crops. A single vine may produce several bushels of fruit one year and only a few fruits most years. Hybrids between *A. arguta* and *A. chinensis* were raised by David Fairchild, but the hybrids never fruited.

Figure 2.—The American cranberrybush in flower. The large white marginal flowers around each cluster are sterile. Only the small inner flowers set fruit.

AMERICAN CRANBERRYBUSH

THE fruit of the native American cranberrybush, highbush cranberry, or pembina (*Viburnum trilobum* Marsh.),[1] is used for jelly making in sections of the northern United States and Canada.[2] From the fruit is produced a jelly rich in color and in pectin but of relatively strong flavor and odor. The fruit resembles that of the cranberry in color and size, but

[1] Formerly known as *Viburnum americanum* Mill

[2] DARROW, G M VIBURNUM AMERICANUM AS A GARDEN FRUIT Amer. Soc Hort. Sci. Proc. (1923), 20 · 44–54 [1924]

——— THE AMERICAN CRANBERRYBUSH Jour Heredity 15 243–253, illus. 1924.

the plants are not related. The fruit of the American cranberrybush is borne on a high bush in clusters, like the elderberry, while the cranberry is borne on a low vine. The American cranberrybush is a close relative of the elderberry and grows to about the same height and in similar clumps with similar flowers (fig. 2). It is sufficiently hardy to grow in the colder parts of the United States. It is often confused with the European *Viburnum opulus* L., which is widely used in the United States as an ornamental, but is readily distinguished from the latter by its clear, acid fruit. The fruit of *V. opulus* is so intensely bitter as to be inedible.

In the spring of 1921 the Bureau of Plant Industry took over for 10 years a plantation of the American cranberrybush established by A. E. Morgan, formerly president of Antioch College, now chairman of the Tennessee Valley Authority, at East Lee, Mass. The plants were the best obtainable selections following a personal survey by Morgan of this fruit in the wild in New

Figure 3.—Three varieties of the American cranberrybush introduced by the United States Department of Agriculture through cooperating nurseries: _A_, Wentworth; _B_, Hahs; _C_, Andrews. The fruit is used for making jelly, which is as rich, red, and firm as that made from the currant and the cranberry.

York and New England and even in Manitoba and Saskatchewan. Fruit was obtained through correspondence from Alaska to Newfoundland.

After a study of the selections at East Lee, and of plants in the wild in various regions, three were named, propagated, and introduced—Wentworth, Hahs, and Andrews (fig. 3). Analyses for acid and pectin and jelly tests by C. A. Magoon, of the Bureau of Plant Industry, indicated that these three were superior to the other selections. They also covered a long season, Wentworth being early, Hahs midseason, and Andrews latest. Through cooperating nurseries these three varieties are now available in the trade. They are propagated by softwood and hardwood cuttings and by layering (fig. 4).

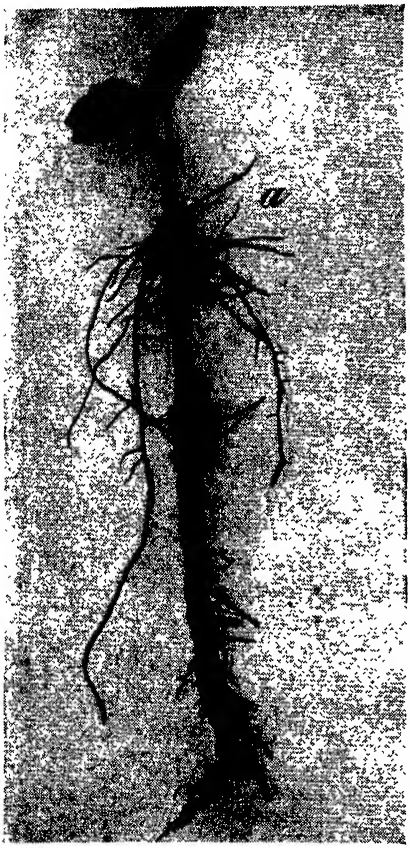

Figure 4.—Propagation of the American cranberrybush by hardwood cuttings. In this case some roots were produced along the cutting, but the largest number came from the base of the new growth (*a*).

Many northern State experiment stations have cooperated with Morgan and the United States Department of Agriculture in testing this fruit, and several are continuing their interest in it. These stations include those in Maine, New Hampshire, Massachusetts, New York, Wisconsin, Minnesota, North Dakota, Montana, and Idaho.

Besides being of value for its fruit, the American cranberrybush is a widely used ornamental, beautiful in flower and fruit, with a rich green summer foliage which becomes highly colored in fall (fig. 5).

Rehder states that there are in all about 120 species of *Viburnum*, nearly all natives of the cooler sections of the Northern Hemisphere. Many are bitter-fruited, many others are sweet-fruited, and some bear clear, acid fruit. It would seem that the viburnums have great promise for the breeder because of their value as ornamentals as well as for fruit production. Species such as *V. carlesii* Hemsl. and *V. fragrans* Bunge are delightfully fragrant, while sterile forms of *V. opulus* L. and *V. tomentosum* Thunb. are the snowballs of commerce. Valuable hybrids would probably result from crossing the Andrews, Hahs, and Wentworth with *V. carlesii*, *V. fragrans*, the evergreen *V. rhytidophyllum* Hemsl., selections of *V. lantana* L. and related sweet-fruited species, the clear acid-fruited *V. wrightii* Miq., and *V. dilatatum* Thunb.

GOUMI OR ELAEAGNUS

GOUMI is the name applied in Japan to several species of *Elaeagnus* grown chiefly for their ornamental value. One species, the cherry elaeagnus (*Elaeagnus multiflora* Thunb., fig. 6, *C*), is also of value for

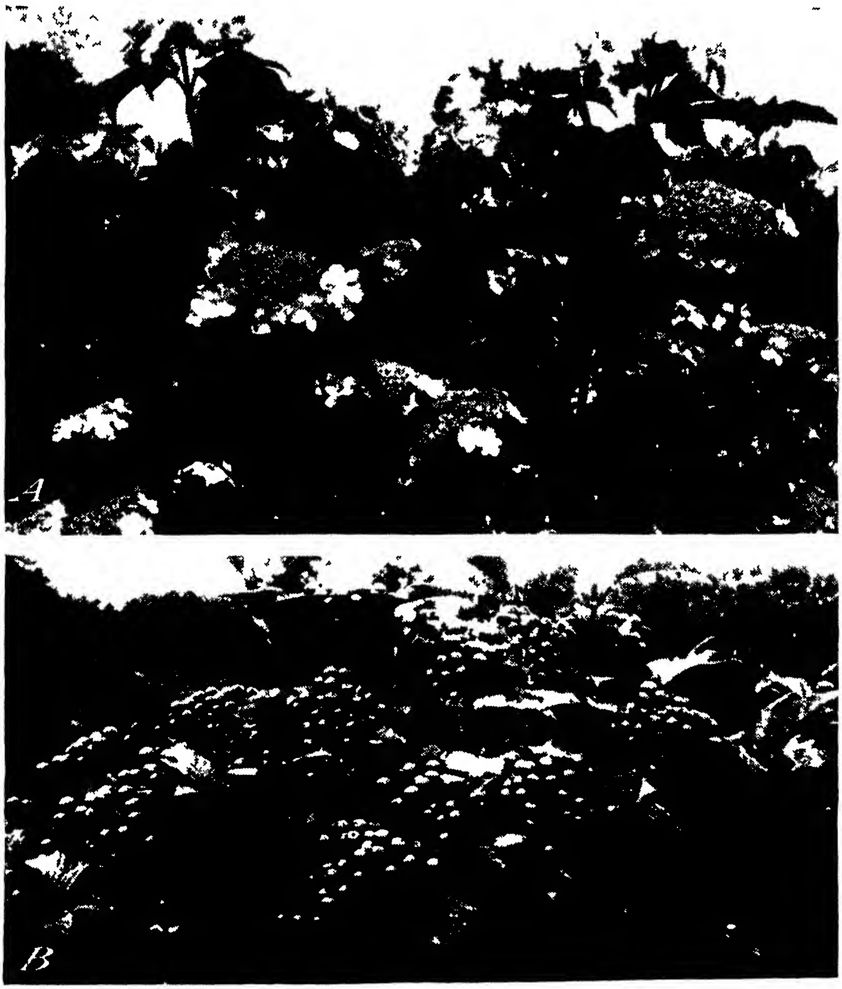

Figure 5.—The American cranberrybush is ornamental in flower (*A*) as well as in fruit (*B*). Both the white flowers and the brilliant red fruit contrast well with the foliage. It is one of the highly prized and widely used ornamentals of the northern part of the United States.

its tart fruit. Another subtropical species, *E. philippensis* Perr., called the lingaro, has produced well in southern Florida. It has edible fruit prized for use in sherbet. Still other species, such as *E. ovata* Serv. (fig. 6, *A*) and *E. umbellata* Thunb. (fig. 6, *B*), bear immense quantities of small fruit.

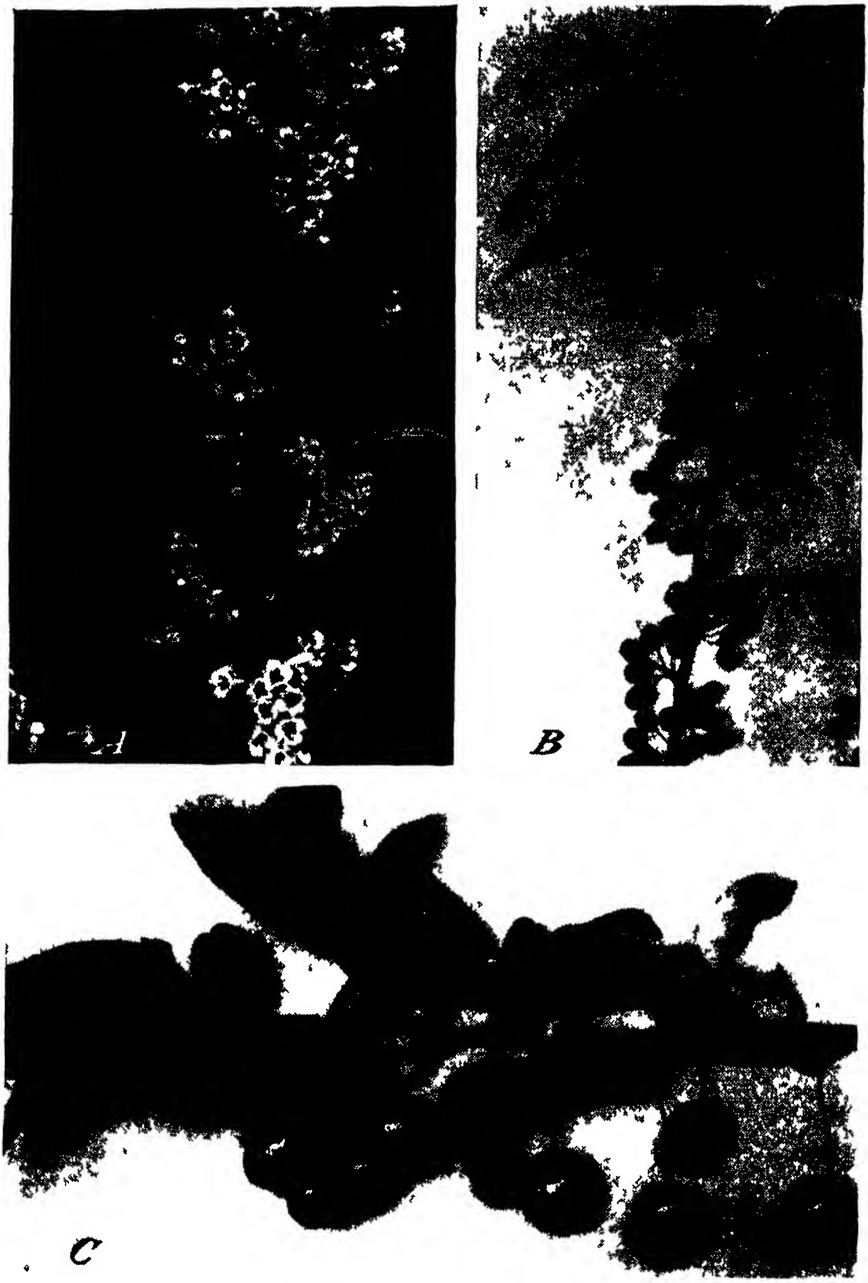

Figure 6.—Elaeagnus or goumi *A*, Flowers of *Elaeagnus ovata*, *B*, fruit of *E. umbellata*, *C*, fruit of *E. multiflora*, the largest-fruited one These hardy, drought-resistant, fruiting shrubs are valuable as ornamentals and as food for wildlife. *E. multiflora* is a valuable food plant of parts of Asia.

Though the cherry elaeagnus was introduced into this country many years ago, it has not become an important fruit even in the garden. The explanation seems to be that it has been almost entirely grown from seed. The seedlings are extremely variable, some producing very little fruit and that small and astringent, others producing abundant fruit as large as cherries and having a pleasant flavor.

Elaeagnus seems worth the attention of the breeder because the fruit is of considerable importance in parts of central Asia, the plants are very hardy and drought-resistant, the seedlings are quite variable, and there are a great many species. A breeding program might include selections of the best fruiting forms from large numbers of seedlings, and hybridizing between species such as *Elaeagnus multiflora*, *E. ovata*, *E. umbellata*, and *E. pungens* Thunb. In the Southern States the fragrant October-flowering species *E. pungens* may be of some value for its fruit and for hybridizing.

ORIENTAL QUINCES

THE oriental or flowering quinces include three species and many varieties, as well as certain hybrids. The best-known species, *Chaenomeles lagenaria* Koidz. (*Cydonia japonica* Pers.), is the so-called Japanese quince, which, however, is a native of central China. It is a spreading shrub with thorny interlacing branches, from 4 to 8 feet high. The dwarf Japanese quince, *Chaenomeles japonica* L., is a sprawling shrub with spiny branches and orange-scarlet blossoms. One hybrid between these two species, named *Chaenomeles superba* Rehd., has blood-red flowers. The flowers of these two species and their hybrids resemble apple blossoms and range from white to salmon and scarlet and even darker. One of the scarlet-flowered varieties most commonly propagated is so covered with flowers in early spring that it is sometimes called "fire bush."

Though ordinarily cultivated for the ornamental value of the bush in flower, the fruit (fig. 7, *A*) is of value for its acidity and pectin content. It has little flavor, but when used in making jelly and preserves with apples, cherries, plums, prunes, and the other cultivated quinces it helps to achieve the balance in the ratio between sugar and acid that is necessary for highest flavor. Tests have been made, in cooperation with the National Preservers Association, to select varieties for this purpose. The variety *grandiflora*, of *Chaenomeles lagenaria*, with fruit 3 to 4 inches in length and weighing one-fourth to one-third of a pound, was the largest and most productive at Glendale, Md., and contained the most malic acid, 5.75 percent.[3] It has apple-pink to rose-pink flowers (fig. 7, *B*).

Because the flowering quinces are largely self-sterile, most people, having only a single bush or only one variety, have never seen the fruit. The varieties *C. lagenaria* var. *baltzii* (cerise-pink flowers), *C. lagenaria* var. *versicolor* (pink flowers), *C. superba* var. *atrosanguinea* (fiery scarlet flowers), *C. japonica* var. *candidissima*, and *C. japonica* var. *nivalis* (white flowers) all bear heavily, and though no tests have been made, some of them may be expected to pollinate the variety *grandiflora* of *C. lagenaria*. Colby,[4] of Illinois, found that *C. lagenaria*

[3] LATHROP, C. P., and WALDE, W. L. THE JAPANESE QUINCE. Fruit Prod. Jour. 7 (4): 14–18, illus.

[4] COLBY, A. S. SOME NOTES ON THE JAPANESE QUINCE. Ill. State Acad. Sci. Trans. (1928) 21: 176–185, illus. 1929.

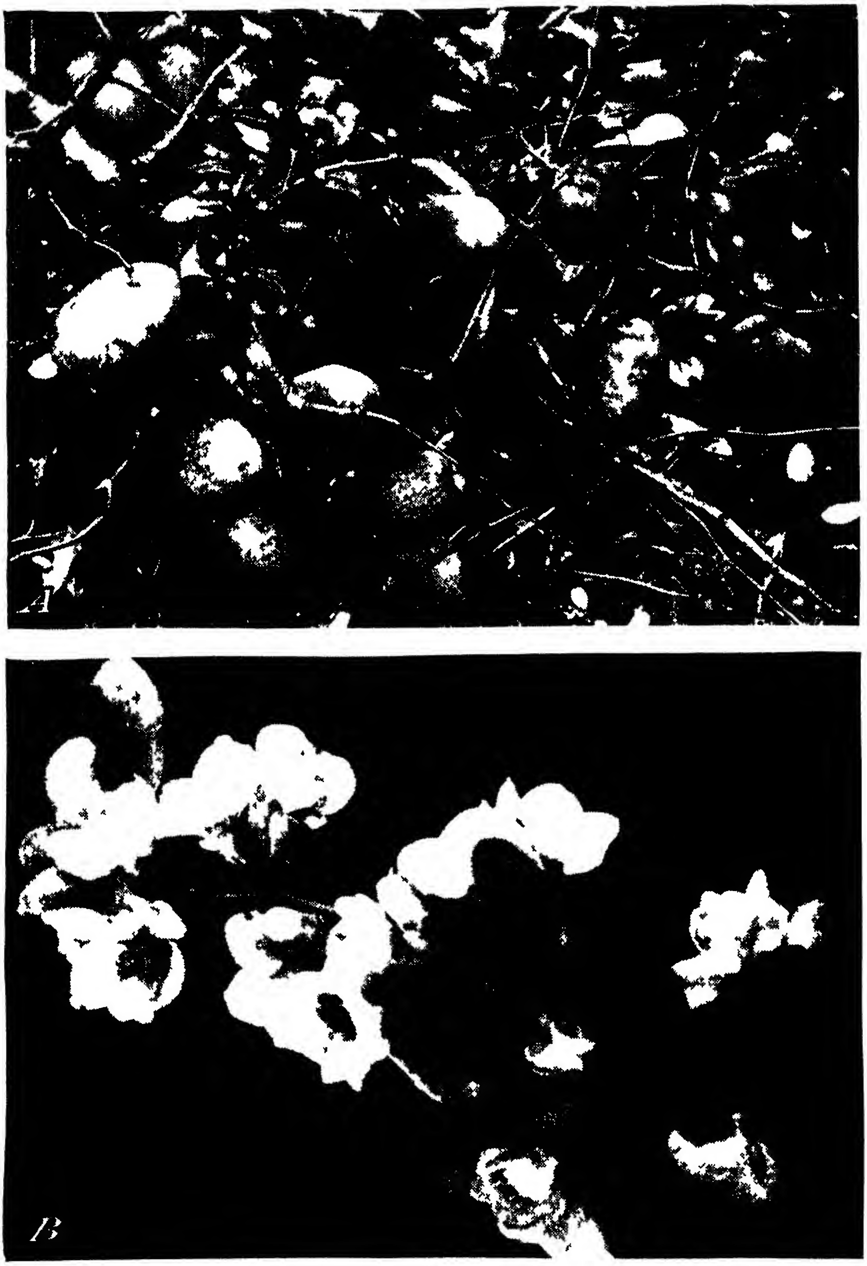

Figure 7.—The flowering quince (*Chaenomeles lagenaria*), a beautiful ornamental but also useful for its fruit (*A*), which is high in malic acid and pectin. *B*, Variety *grandiflora*, propagated originally for its apple-pink flowers but bearing very large fruit of very high acid and pectin content.

var. *grandiflora* was at least partly self-fertile, but no other variety that he tested was at all self-fertile. He has found the fruit of *C. lagenaria* var. *versicolor* fully as large as that of the variety *grandiflora* under his conditions.

The fruits of several varieties are fragrant and are used to perfume rooms. Colby lists the varieties *baltzii* and *atrosanguinea* as having much perfume. The Chinese cover the fruits with a coat of thin oil and keep them in the houses a long time.

Another species from China, *Chaenomeles sinensis* Koehne, is a small tree bearing its flowers singly and having fruit of enormous size, up to 6 inches or more in length. Though its fruit may also be used as a source of acid, it is coarser and has less acid and pectin than the other species. It has a strong flavor, and a small proportion will impart a pleasing suggestion of quince to jelly and preserves made from milder flavored fruits. It is very fragrant and is also used to perfume rooms. The foliage turns a brilliant scarlet in the fall, making it desirable for tall hedges and for ornamental plantings.

The two flowering species, *Chaenomeles lagenaria* and *C. japonica*, are hardy as far north as Massachusetts, New York, and Illinois, and may be raised southward to northern Georgia, or as far south as there is sufficient winter cold to break their rest period. The other species, *C. sinensis*, is hardy north to Philadelphia and may be raised in the South nearly to the Gulf of Mexico.

So far, improvement in the fruit characters of this group has been largely accidental. The high acidity and pectin content of the fruit of some varieties suggests that attempts to obtain still larger amounts would be desirable. Improvement might be made by developing larger sized and more handsomely colored fruit in varieties adapted to different regions, by securing more open growth so that the fruit can be picked more easily, by eliminating thorns on the bushes, and by developing self-fertile varieties. So far no hybrids with the European cultivated quince are known, but attempts should be made to produce them.

The possible importance of this fruit in the preserving industry is indicated by the following quotation from Lathrop and Walde:[5]

> Were a preserver to name the properties most needed in a new fruit by the preserving industry today, he would unwittingly be describing the Japanese quince * * *. * * * its bid for recognition and economic importance is not based upon its becoming a new, distinctive-flavored product. It serves a very different purpose:—to supply a non-flavored fruit, or fruit juice, very high in l-malic acid and pectin to those popular flavored fruits as the apple, cherry, European quince, and plum or prune when requiring additional l-malic acid. * * * These familiar flavors of jellies and preserves when they reach the consumer in many instances do not show off to their best advantage. * * * the marked effect and advantage of making small, definite additions of fruit acid in jellies and preserves was described in the case of some fruits to bring out more of the total fruit flavor actually present.

CHINESE AND OTHER BUSH CHERRIES

THE Chinese bush, Manchu, or Nanking cherry, *Prunus tomentosa* Thunb. (called by the Chinese the mountain cherry),[6] has been grown in the United States some 50 years as an ornamental shrub but now

[5] LATHROP, C. P., and WALDE, W. L. See p. 14 of reference cited in footnote 3.
[6] DARROW, G. M. THE CHINESE BUSH CHERRY . . . Jour. Heredity 15: 169–176, illus. 1924.

is attracting attention for its fruit. It is one of the earliest of all shrubs to flower in the spring, its white to pink blossoms (fig. 8) opening just as the leaves start to unfold and its brilliant red fruit

Figure 8.—Flowers of the Chinese bush cherry. It flowers on the previous season's growth.

(fig. 9) ripening with the last of the strawberries. The fruit has a range in flavor and texture from the sweet to the sour cherry with a peculiarly attractive tang. It is as large as the wild cherries of

Europe, from which the cultivated sweet and sour cherries have originated. The foliage is resistant to the common cherry leaf troubles. The tree is cultivated to some extent in China, and the fruit is also gathered in the wild and sold in the markets. The range of the Nanking cherry in Asia is from southern Manchuria to the Kashmir region of northern India, a region for the most part semiarid and in latitude and climate comparable to the territory from eastern New Mexico northward to North Dakota.

Figure 9.—The Chinese bush cherry in fruit. Its brilliant red fruits range in flavor from the sweet to the sour cherries. They are produced in great abundance provided they escape spring frosts and brown rot. Objectives in breeding this fruit should include late-flowering, brown rot-resistant seedlings.

When they escape spring frosts and severe attacks of brown rot, the bushes are loaded with fruit of the size of small sour cherries. The most needed improvements are the introduction or discovery of late-flowering and brown-rot-resistant seedlings (fig. 10). The brown rot fungus often kills back twigs and branches in humid sections.

Harlow Rockhill, strawberry breeder at Conrad, Iowa, has crossed the Nanking cherry with the western sand cherry, *Prunus besseyi* Bailey, and has grown several generations of hybrid seedlings. He feels that some are very promising for Iowa conditions, as they flower later and are less often injured by cold than the Nanking cherry. Importations are needed from different regions to make selections adapted for the coldest to the warmest, and the driest to the most humid regions of this country. Rockhill has crossed the Nanking cherry with the Napoleon (Royal Anne), Montmorency, and Zumbra cherries, and there is the possibility of obtaining hybrids with many other cherries. The Arnold Arboretum reported having a natural hybrid between *P. tomentosa* and *P. triloba* Lindl. in their plantings.

Slate,[7] of the New York (State) Agricultural Experiment Station, has selected fine fruiting seedlings at Geneva and has started propagating them. By and large, it is a promising fruit for the plant breeder, and it may have commercial possibilities.

Figure 10.—Seedling plants of the Chinese bush cherry, in the middle an early flowering, at the right a later flowering, and at the left a much later flowering sort. These seedlings illustrate the possibility of obtaining much later flowering selections that may escape unseasonable frosts.

Prunus glandulosa Thunb. and *P. japonica* Thunb. are very hardy dwarf shrubs that are ornamental and have deep red to purple-black fruits useful for pies, jellies, and sauce. There are also many other species of bush cherries in Asia that may be worth using in breeding. Besides the bush cherries, *P. triloba*, classed as a flowering almond, is possibly a still more beautiful hardy flowering and fruiting shrub with flowers of pure pink.

[7] SLATE, G. L. THE IMPROVEMENT OF PRUNUS TOMENTOSA. Amer. Soc. Hort. Sci. Proc. (1929) 26: 28–31. 1930.

IMPROVING THE WILD BLUEBERRY

FREDERICK V. COVILLE, Principal Botanist, Division of Plant Exploration and Introduction, Bureau of Plant Industry

IN 1906 the writer began a series of experiments to learn the fundamental facts in the life history of the blueberry, which might serve as a basis for the possible cultivation of this delicious wild fruit. It took 2 years to find that the blueberry plant requires an acid soil. These experiments showed also that trailing-arbutus, rhododendrons, azaleas, mountain-laurel, pink ladyslipper, and many other plants require acid soils.

Although every gardener today knows that blueberries, as well as hundreds of other kinds of plants associated with blueberries in their wild habitats, thrive only in acid soil, that fact apparently was not known to American horticulturists prior to these experiments with blueberries. The Cyclopedia of American Horticulture, published in four volumes in 1900, and prepared with the collaboration of more than 200 horticulturists and botanists of the United States, contains no mention that an acid soil is required for the successful cultivation of any one of these plants.

Figure 1.—Frederick V. Coville, assistant botanist and principal botanist, United States Department of Agriculture, 1888–1937; first breeder of blueberries and founder of the industry of blueberry culture.

BEST WILD BLUEBERRIES CHOSEN FOR BREEDING PURPOSES

AFTER the soil-acidity requirement of blueberries had been determined, 2 years more were devoted to further studies of the life history of the blueberry, and by the end of 1910, when the first bulletin was published,[1] the blueberry had been grown successfully from seed to fruit; selected plants had been propagated by grafting, budding, division, layering, twig cuttings, and root cuttings; methods of pollination had been devised and applied; and wild plants with superior fruit had been chosen as the basis for breeding experiments.

[1]COVILLE, F. V. EXPERIMENTS IN BLUEBERRY CULTURE. U. S Dept Agr., Bur Plant Indus. Bull. 193, 100 pp, illus. 1910.

DR. COVILLE *died suddenly on January 9, 1937, only a few weeks after he had completed the article that appears herewith. It is fitting that his last paper deals with the greatest of his achievements in agriculture. His work in domesticating and improving the blueberry was based upon years of taxonomic, physiological, and genetic investigation of the wild blueberries of the eastern United States, and the flourishing industry fathered by his efforts rests upon a sure foundation of scientific knowledge.*

Yet the blueberry achievement is but one of many in his chosen science, botany. In 1888, the year after his graduation from Cornell University, he entered the Department of Agriculture, and in 1891 he accompanied the famous Death Valley expedition in the capacity of botanist. As a result there was published in 1893 Botany of the Death Valley Expedition, one of the classics of the study of desert vegetation. Soon Coville was back again in the far West, investigating the useful plants of the American Indians and carrying on, in collaboration with the foresters of the Department, fundamental studies of the grazing and browse plants of the national forests. The present grazing-management policies of the Forest Service are the outcome, in large measure, of these investigations.

No one who had the privilege of being in the field with Dr. Coville could fail to be impressed by his keenness of observation and his constant appreciation of the beauty and the human appeal as well as the scientific interest of plants. The few examples of his work mentioned in the preceding paragraphs give only a partial view of his wide-ranging interest. He published no fewer than 158 scientific papers. Aside from his own special investigations, he played a leading part in such enterprises as organizing the research work of the National Geographic Society, establishing the Desert Botanical Laboratory of the Carnegie Institution of Washington, and founding the National Arboretum. With F. L. Olmsted and H. P. Kelsey, he edited that indispensable aid of the horticulturist, Standardized Plant Names. The writer well remembers Coville's delight, while the book was in preparation, when he or one of his colleagues would hit upon an apt and attractive English name for some plant hitherto known only in Latin or Greek.

Dr. Coville had a host of friends in all walks of life, to whom he was a patient and kindly counselor. Because of his reputation for sturdy good sense, people sought his advice, and he never begrudged for this purpose time that he could ill spare from his many occupations. The deep sense of loss his colleagues feel at his death is intensified by regret that he did not live to make one more trip to Death Valley, the scene of his first important botanical discoveries, as he had planned to do this spring. The popular flora of the Death Valley region he was engaged in writing would have been a most appropriate conclusion of a busy, useful, and happy life.

T. H. KEARNEY.

Brooks Blueberry

The first wild blueberry selected for breeding purposes was Brooks, named after the owner of the pasture at Greenfield, N. H., in which the plant was found. It was a highbush blueberry, *Vaccinium corymbosum* L. The berry was discovered in July 1908, after three summers of cursory observation in the mountains of southern New Hampshire and 3 weeks of diligent search in the summer of 1908. The bush grew at an elevation of 950 feet above the sea. It stood with many other blueberry plants in an old, brushy, mountain pasture, in acid and permanently moist but not swampy soil. It was about 7 feet high, and the largest of the several stems was about 2 inches in diameter. The plant was old, and the tops on some of the stems were partially dead. Other parts of the bush were in full vigor, with robust twigs and foliage. It yielded 3 quarts of berries. The berries were of large size, reaching a diameter of more than half an inch. The flesh was firm and juicy. The color was an unusually light blue, due to a dense bloom over the nearly black surface. In flavor the berry was exceptionally good. It was sweet, but sufficiently acid to be decidedly superior to the mild-flavored fruit of the lowbush blueberry, *V. angustifolium* Ait., yet not sour like the Canada blueberry, *V. canadense* Kalm, and it possessed in a high degree the flavoring ester that is the special characteristic of the best wild blueberries of New England. The delicious flavor of this wild blueberry from New Hampshire appears in all the cross-bred named varieties of blueberries except Jersey and Wareham, and the flavor of those two varieties would be more delicious if Brooks had been included in their ancestry.

This description of the Brooks blueberry has been given in detail because I regard its selection as of fundamental importance to the success of the Department's blueberry-breeding experiments. Every breeder of race horses or of milk cows understands that the choosing of the individuals to be interbred is of the highest importance. Plant breeders usually select carefully the species they intend to interbreed, but often make the mistake of paying too little attention to the choice of superior individual plants within the species.

ATTEMPT TO IMPROVE THE BLUEBERRY THROUGH SELF-POLLINATION A FAILURE

The first attempts to improve the blueberry by breeding were made in 1909 and 1910, when flowers on the original Brooks bush, and on plants propagated from it by grafting, by budding, and by cuttings, were pollinated by hand with Brooks pollen. These flowers did not set fruit, or the fruit withered and dropped long before it was mature, or if a few berries ripened they contained abnormally few seeds, most of these lacking embryos. No plants resulted from the sowing of these seeds. In later years self-pollination was tried repeatedly. In some instances a few plants were obtained from the few seeds resulting from such pollinations, but the plants were weak and they never produced fruit that was either desirable or abundant. This method of breeding, therefore, so successful with corn and with beans, was finally abandoned as a means of improving the blueberry. Before this subject is dismissed, however, it may be well to cite an experiment

in 1914 which shows how definite is the tendency to failure in self-pollination as compared with cross-pollination in the blueberry. On February 23 to 28 of that year 20 flowers on a hybrid blueberry plant known as 393C were pollinated with pollen from another hybrid blueberry, 394Y. Nineteen of these twenty cross-pollinated flowers set fruit and 19 berries ripened. On February 27 and 28, six flowers on 393C were pollinated with the plant's own pollen. From these six self-pollinated flowers no berries ripened. Five of the six flowers set fruit at first, but these all shriveled and dropped while they were still young and green. The failure of 393C to produce seeds when pollinated with its own pollen was not due to sterility of the pollen, for the pollen of this plant, when used in another experiment, on 394Y, yielded an abundance of berries and seeds from which many vigorous and productive plants were grown

NUMBER OF CHROMOSOMES IMPORTANT

ANOTHER series of failures in the early blueberry pollinations was due to a cause quite different from self-sterility. Certain species of blueberry usually yielded no fruit when cross-pollinated, among them the lowbush blueberry and the Canada blueberry, species of similar size and habit, which occur together in enormous areas on both sides of the Canadian border; the highbush blueberry and the bigbush blueberry, *Vaccinium atrococcum* (A. Gray) Heller, which resemble each other so closely that Asa Gray considered one a variety of the other; and the highbush blueberry and the dryland blueberry, *V. vacillans* Kalm. When the two species of any of these pairs were cross-pollinated they usually produced no fruit. If, however, any berries resulted from the cross-pollinations, their few seeds produced weak and unproductive plants. In later years, cytological studies by Longley [2] showed that in each of these pairs the first-named species has 24 chromosomes; the other 12 The 12-chromosome species, it was found later, cross freely with each other. They even cross with the deerberry, which belongs to a related genus, *Polycodium*, but which has 12 chromosomes.

Among the 24-chromosome species of blueberry, crosses could be made easily, notwithstanding great differences in the physical appearance of the two species that were crossed. Not only were the highbush and the lowbush blueberry hybridized by artificial pollination, but natural hybrids between them are of frequent occurrence in New England pastures. The highbush blueberry grows to a height of 7 feet, with many stout stems in a single clump, and its leaves are commonly 2 to 2½ inches long by 1 to 1½ inches wide, the margins usually without teeth. The lowbush blueberry is 6 inches to a foot in height. It spreads by slender rootstocks into broad patches, and its leaves are small, narrow, and finely serrate. The highbush blueberry is easily crossed also with the myrtle blueberry of Florida, *Vaccinium myrsinites* Lam., a 2-foot species with evergreen, minutely-toothed leaves, which are seldom more than three-fourths of an inch in length. The highbush blueberry can be crossed easily also with the hairy blueberry, *V. hirsutum* Buckl., a southern-Appalachian species 2 to

[2] COVILLE, F. V BLUEBERRY CHROMOSOMES Science (n s) 66 565 566 1927
LONGLEY, A E CHROMOSOMES IN VACCINIUM Science (n s) 66 566–568, illus. 1927.

3 feet high, with leaves densely pubescent on both surfaces, and with hairy, black berries. In a word, ease of crossing, among blueberry species of the eastern United States, is dependent on equality of chromosome number. Blueberry species of the most diverse appearance and characteristics, but with the same number of chromosomes, hybridize readily.

Russell Blueberry

The second wild blueberry selected for breeding purposes was Russell. It was brought to my attention in 1909 by Frank Russell as the best lowbush blueberry on his 600-acre mountain farm at Greenfield, N. H. The original plant had become so shaded by the low branches of a young oak tree that it no longer produced fruit, but in the greenhouses at Washington its berries reached a diameter of over nine-sixteenths of an inch. The berries were light blue in color, and they ripened earlier than those of Brooks. This tendency toward earliness appears in all the progeny of the Russell blueberry and is of great commercial importance because the earliest of the improved blueberries often bring the highest prices.

FIRST BLUEBERRY HYBRIDS

The first cross-pollinations between Russell and Brooks were made in the spring of 1911. Some of the resulting first-generation hybrids were cross-pollinated with each other in 1913. The resulting progeny, about 3,000 hybrids of the first and second generations, was grown to maturity in the field, with remarkable results.

The outstanding characteristic of these hybrids was the variation in the color of their fruit The berries of both Brooks and Russell are of light blue color. The body of the berry in both varieties is a dark purple, which appears as a black when the bloom is rubbed off. In the first-generation hybrids of Brooks and Russell the bloom was much thinner than in either parent, and in consequence the berries of the hybrids were dark blue in color, in strong contrast with the light blue berries of both parents. One of these first-generation hybrids is shown in figure 2. When two of these dark-berried first-generation hybrids were interbred the resulting second-generation hybrids showed a still more remarkable diversity of color. On about 65 percent of the plants the berries were dark blue, just as in the first-generation hybrids. On about 18 percent they were black, some of them a dull black, some without a trace of bloom, so that the berries had the shining appearance of a black shoe button. On about 15 percent of the plants the berries were light blue, like the berries of both grandparents. On about 1.5 percent the berries were albinos. They lacked the purple coloring matter that, located in the skin of the blueberry, gives the fruit the black color that appears when the bloom is rubbed away. Further comments on these albino blueberries are given later in this paper under the varieties Redskin and Catawba. On about 0.5 percent of the plants the heavy bloom of the berries on the two grandparents was replaced by an apparently still denser and lighter colored bloom which gave the berry a metallic luster like that of new aluminum ware.

A shining black color in these blueberry hybrids was never found associated with a delicious taste, perhaps because there was not a

sufficient number of such plants to afford an adequate range in flavor. The same was true of the "aluminum" berries. In the dark-colored berries excellent flavor and good size were often combined. These

Figure 2.—One of the first blueberry hybrids. This is a first-generation cross between a wild highbush blueberry, Brooks, and a wild lowbush blueberry, Russell, from Greenfield, N. H. Another hybrid of the same parentage, 394Y, was one of the ancestors of the varieties Rancocas, June, and Weymouth. (Natural size.)

dark-berried bushes of 2- to 3-foot stature are of frequent occurrence in New England pastures as natural hybrids between *Vaccinium corymbosum* and *V. angustifolium.* Such a hybrid is the plant described in Gray's Manual of Botany and Rehder's Manual of Cul-

tivated Trees and Shrubs as *V. corymbosum amoenum.*[3] About Greenfield, N. H., the plants of such hybrids are popularly known as the half-high blueberry. For many years I regarded this plant as a distinct species, until it appeared by hundreds among the artificial hybrids.

Sooy Blueberry

An important step forward in blueberry breeding came about by enlisting the interest of wild-blueberry pickers in New Jersey through cooperation with Elizabeth C. White, of New Lisbon, N. J. On July 20, 1911, I stopped at the house of Ezekiel Sooy, an experienced picker of wild blueberries, living at Browns Mills. It had been stipulated that a wild blueberry, to be valuable, must be half an inch in diameter. Mr. Sooy said that he hadn't any half-inch blueberries for me, that all the good bushes had berries much larger than that. He proceeded to take me to one of them, near the road, a mile east of his house. The berry proved to be a beauty, five-eighths of an inch in diameter. I started to arrange that a portion of the bush be taken up later when the plant was dormant, but Mr. Sooy took hold of a rooted sucker about an inch in diameter and ripped it from the ground with a forceful yank. I had been in the habit of treating blueberry plants with consideration and when I protested that the plant had been taken up neither at the proper season nor in the proper manner, Mr. Sooy said, "That root will grow. You can't kill a blueberry bush." So the top was cut off and the root was wrapped in a wet newspaper and taken to Washington, where under the name Sooy it became one of the progenitors of some of our best blueberry hybrids.

Brooks and Sooy were cross-pollinated in 1912. Nearly 3,000 seedlings of this parentage were grown to maturity in the field. Among them were two plants that when propagated from cuttings became the improved blueberry varieties Pioneer and Katharine

THOUSANDS OF PEDIGREED SEEDLING BLUEBERRIES TESTED TO OBTAIN 15 NAMED VARIETIES

Up to the year 1936 about 68,000 pedigreed blueberry seedlings have been fruited and carefully examined to determine which were sufficiently valuable to be propagated and distributed as named varieties. The ancestry of each seedling is a matter of record. In the testing plantations it was sometimes evident from the characteristics of an individual plant that it did not belong to the group indicated by the record. Somewhere during its life, when it was placed in the ground as a seed, or when it was potted in the greenhouse, or when it was packed for shipment, or when it was placed in the field nursery, or when it was set in its final place in the testing field, it was exchanged with another plant that had a different history. It happens, however, that none of these evidently misplaced plants has proved to be of such high quality that it deserved to be named. We are able to say, therefore, that the ancestry of our named varieties of improved blueberries is above suspicion.

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[3] Gray, A. Manual of Botany of the Northern United States. Ed 6, 760 pp, illus New York and Chicago. 1890

Rehder, A. Manual of Cultivated Trees and Shrubs Hardy in North America, Exclusive of the Subtropical and Warmer Temperate Regions. 930 pp., illus. New York. 1927.

TESTING BLUEBERRIES

The selection of the few best plants in a field containing thousands of individual pedigreed blueberry seedlings is a tedious business. It requires sustained attention and keen and repeated observations. As one walks down the rows, the desirable color of an exceptionally light-blue berry can be observed almost at a glance. If, however, the branches of the plant are unusually flexible, the wind swaying a heavy cluster of berries against a neighboring branch may wipe away the bloom and disfigure the berries by leaving them black on one side. Stiffness of branch is needed to insure uniformity in the color of the berries.

To be sure of the size of a blueberry, one's judgment needs to be checked continually with a gage. The gage illustrated in figure 3 was in use for several years until its largest hole, 25 millimeters (an inch is 25.4 mm), was found to be too small to measure the largest hybrid blueberry. This is the one described later in this paper as GM37 and illustrated in figure 4. The original Brooks blueberry slightly exceeded 14 mm, the Russell blueberry 15 mm, and the Sooy blueberry 16 mm. Our largest hybrid that has a delicious flavor has thus far attained only 24 mm in diameter.

The ease of picking and the size of the scar on the blueberry where it separates from its stem are important. A small and dry scar is the most desirable, and such a scar is usually associated with ease of picking. Further notes on difficulty of picking are given later under the variety Katharine, and on ease of picking under the variety Rancocas. An undesirable feature was observed in some of the seedlings when the joint at the base of the stem of the individual berry separated more easily than the joint at the upper end of the stem, and the stem therefore remained attached to the berry when it was picked. Such a berry is undesirable commercially.

In many of the seedlings the skin at the base of the blueberry tends to remain attached to the stem and, in picking, a piece of skin is torn from the berry. A seedling bearing such berries is always rejected, however good its flavor and other qualities.

The keeping quality and the firmness of flesh must be considered in selecting a blueberry, because under commercial conditions berries without these qualities may not reach the consumer in good condition. A blueberry is often rejected if it has a very large calyx. Such a calyx may afford a place for an insect to hide.

Occasionally the ripe fruit of a blueberry tends to crack after a rain. The crack may come between the calyx lobes, where the skin is sometimes tightly stretched as the berry enlarges and ripens, or it may form about the middle of the berry. Several blueberries of large size and delicious flavor have been rejected because of their tendency to crack.

Testing for Flavor

Probably the most elusive and difficult thing to judge in a new blueberry is its flavor. After several hours of tasting, all blueberries taste alike, and they all taste sour. On a day in which many blueberries are to be tried for flavor, I never swallow the berries I am tasting, and I taste only those that appear promising from their size

and other visible qualities. Even with such precautions to conserve one's ability to distinguish flavors, it sometimes is necessary to stop work in the field until one's organs of taste have recovered their faculty of discrimination. If a blueberry is to be eaten in a pie, its flavor is of secondary importance, for if it has not sufficient acidity a teaspoonful of vinegar, or its equivalent in lemon juice, will supply the deficiency; but if the blueberry is to be eaten as a fresh fruit, either out of hand or with cream and sugar, its flavor, its seedlessness, and its succulence are its chief contributions to enjoyment.

A blueberry is sweet, slightly sweet, or quite without sweetness. It may be sour, slightly acid, or flat. It may have none of the special flavor of the blueberry, or a little of it, or this flavor may be present in a high degree. Its flesh may be lacking in juiciness, or it may be juicy and sprightly. When taken directly from the bush, the blueberry varies in taste with its degree of ripeness. When blueberries first turn blue they usually are still sour. When they have been blue about a week they commonly are ready for picking, but the berries of some of the varieties with relatively sour fruit may need to remain on the bush for 2 or even 3 weeks after they turn blue, before they become really palatable.

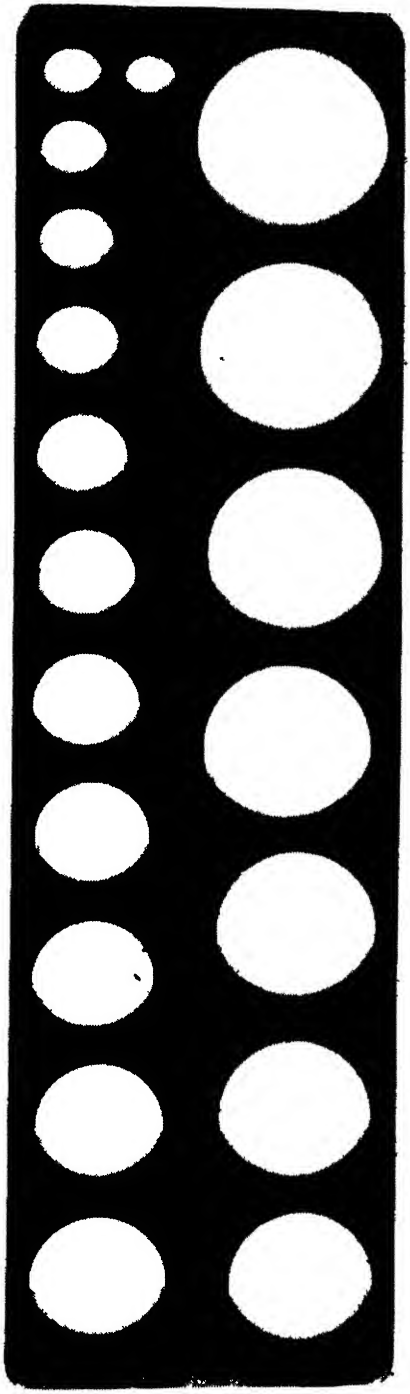

***Figure 3.*—A blueberry gage, the holes from 7 mm (a little more than a quarter of an inch) to 25 mm (a little less than an inch) in diameter. The largest blueberry thus far grown is a little larger than the largest hole in this gage.**

Individual preferences vary regarding the taste of blueberries. Some persons prefer a blueberry so sour that it cannot be eaten without liberal quantities of sugar. My own preference is for a blueberry that is juicy, sweet, with a slight acidity, and with the characteristic blueberry flavor highly developed. If such blueberries are sound, and for about 2 days after picking, can be kept in a shady, breezy place, without refrigeration, preferably until they have begun to shrivel very slightly, they are then in their ideal condition for flavor, and are ready to go into the refrigerator for chilling before they are served.

In the field it has seemed difficult to find a satisfactory flavor in a blueberry on a very hot day. Whether the fault is with the blueberry or with the taster I cannot say. In tasting blueberries in the field, one may easily make an error of judgment if the berry he tastes is blue but not really ripe. If the berry is in an underripe condition it will have a purplish color around the scar where it separated from its stem. If the berry is of normal color and is fully ripe the area around the scar will be of the same color as the rest of the berry.

To avoid the introduction of new blueberry varieties that are chiefly valuable to the grower only, because of their productiveness and their shipping quality, it has been the aim of the Department, in its blueberry breeding, to consider the consumer also, and especially to develop for his benefit varieties of high flavor. As evidence of the faithfulness of this endeavor it may be recorded that more than 300 seedling blueberry plants that bore berries over three-quarters of an inch (19.1 mm) in diameter have been destroyed because they did not come up to the standards we have set for flavor.

PROPAGATING NEW VARIETIES

When a seedling is of such high quality that it is considered worthy of propagation and distribution as a new and named variety, single buds taken from it are inserted, in midsummer, near the base of new shoots that have grown from older blueberry plants cut to the ground in the preceding winter. In the following spring each shoot is cut off just above the inserted bud, and no other bud is allowed to grow. By the end of the season the plant has a top of nearly the same size as the top that was cut off two seasons before, and this new top furnishes many cuttings of the new variety. By this procedure a new variety of blueberry can be propagated many times more rapidly than if the cuttings were taken directly from the single original plant.

THE IMPROVED VARIETIES OF BLUEBERRY

Pioneer

Pioneer was so designated because it was the first named variety developed as a result of blueberry breeding. It was a first-generation cross between the wild highbush blueberries Brooks and Sooy, made in 1912. Like all the improved varieties not otherwise described, its leaves have no teeth on their margins. Its berries are of light blue color, sweet, of excellent flavor, and when fully ripe are without acidity. The largest berry on the original bush was 18.5 mm in diameter. Young Pioneer plants in commercial fields have borne berries up to 19.7 mm. Pioneer is a midseason variety.

Greenfield

Greenfield was a second-generation hybrid between Brooks, a highbush blueberry, and Russell, a lowbush blueberry, both of them wild plants from Greenfield, N. H. The leaves of Greenfield were finely toothed. The seed from which the plant was grown came from a cross-pollination made in the spring of 1913. The variety never became established in commercial blueberry culture, and is recorded here only for the purpose of accounting for the name.

Cabot

The Cabot blueberry is a first-generation hybrid between two wild highbush blueberries, Brooks, already described, and Chatsworth, which was found near the settlement named Chatsworth, in the pine barrens of New Jersey. The cross-pollination was made in 1913. The bush was named for my son, Cabot Coville, now secretary of the American embassy at Tokyo, who chose this bush for the flavor of its berries, which have a slight acidity, in preference to the sweet, nonacid berries of Pioneer. Cabot is an early variety, for many years the earliest of the named varieties, and in consequence it has been planted very extensively by blueberry growers. It has been found desirable to pick its berries about twice a week, and a bush sometimes yields as many as seven pickings. The berries on the original bush reached a diameter of 18.5 mm. For some obscure reason the fruit buds of the Cabot blueberry, in late winter, are a morsel fascinating to deer. At the blueberry plantation known as the Ore Ponds, a few miles west of Toms River, N. J., the deer almost denuded the Cabot bushes of their fruit buds in the early spring of 1928. In consequence of this excessive pruning by deer, the remaining buds produced berries up to 20.5 mm in diameter, an unusually large size for this variety.

Katharine

The Katharine blueberry is of the same parentage as Pioneer. It was a first-generation cross between the wild highbush blueberries Brooks and Sooy, from a pollination made in 1913. The berries are light blue and of especially delicious flavor. On the original bush they reached a diameter of a little over 19 mm. Occasionally in commercial plantations they reach 20 mm. The Katharine is hard to pick. The berry clings tenaciously to its stem, and when it is pulled away a hole is often torn in the base of the berry. The injury detracts from both the appearance and the keeping quality of the berries, yet in spite of this defect the Katharine is a variety that has been very satisfactory to the consumer. The Katharine is named after my daughter, Katharine, now Mrs. Chester C. Woodburn, of Des Moines, Iowa, who in one of her high-school years did all my blueberry pollinations. The variety ripens a little later than Pioneer.

Rancocas

One of the parents of Rancocas was an unnamed blueberry hybrid known as 394Y, a first-generation cross between Brooks and Russell. The other parent was a wild blueberry from the pine barrens of New Jersey named Rubel. This is, in form, the German spelling of the

name of the old Russian coin, the rouble. The name of the blueberry variety Rubel, however, is of neither German nor Russian derivation. The man who discovered this bush was Rube Leek. Rube did not seem an expressive name for a berry that was blue and beautiful, and Leek was suggestive of a flavor that the berry did not possess. Rubel was a compromise, made up of Mr. Leek's first name and the initial of his last. The seed from which the Rancocas bush grew was the result of a pollination in the spring of 1915. Rancocas is a second-early variety, ripening its berries later than Cabot and earlier than Pioneer. The original bush bore berries up to 18 mm in diameter. Berries in commercial plantations sometimes exceed 19 mm. Rancocas tends to the production of heavy crops on young and healthy bushes, so heavy indeed that unusual care must be taken to prune the bushes severely in order to insure a good crop in the following year. The leaves of Rancocas have finely toothed margins. The berries have a small, dry scar and are very easily picked. The name of this variety came from Rancocas Creek in New Jersey. Near this creek was the blueberry plantation in which the variety gave its first satisfactory performance.

Jersey

The variety Jersey was so named because both its parents were wild plants from New Jersey. These parents were Rubel, already described under Rancocas, and Grover, discovered by Russell Grover. The two were cross-pollinated in 1916. Jersey is a variety maturing late in the season, so late in fact that its berries often bring a high price, in northern plantations, because of its lateness. This and other late varieties extend the blueberry-picking season over a period of about 8 weeks, the early varieties beginning to ripen in New Jersey in the latter part of June and the late varieties continuing until the middle of August and sometimes later. The berries of Jersey are large, up to 22.4 mm in diameter, and, until dead ripe, too acid for the taste of most persons. Jersey is of remarkably robust growth, the leaves on vigorous shoots sometimes attaining a length of 4 inches and a width of 2¼ inches.

Concord

The Concord blueberry was so named because of its large clusters of berries, which, all ripe at the same time, resemble clusters of Concord grapes. It is a first-generation hybrid between the wild highbush blueberries Brooks and Rubel and came from a cross-pollination in 1917. The original bush bore berries up to 18 mm in diameter. In field culture its berries sometimes reach a diameter of 20 mm, occasionally 21 mm. Concord berries are delicious when they are allowed to remain on the bush until they are fully ripe and have lost the excessive acidity they possess when they first turn blue. Concord is a midseason variety, ripening at about the same time as Pioneer.

June

June, named for its early ripening in New Jersey, is of the same parentage as Rancocas, but from cross-pollinations made in 1919. On the original bush the berries reached a diameter of 20 mm. In commercial plantations they have sometimes exceeded 21 mm. The berry

is of medium blue color, sweet and delicious when fully ripe, with a slight subacidity. It usually ripens earlier than Cabot. Although June is of one-fourth lowbush ancestry, its leaf margins do not have the teeth that characterize its lowbush grandparent.

Scammell

The Scammell blueberry is named for H. B. Scammell, of Toms River, N. J., who first showed how good are the qualities of this berry under field conditions. One of the parents of the Scammell was a cross between the wild blueberries Brooks and Chatsworth. This Brooks-Chatsworth parent, which was never planted in the field, was recorded in the greenhouse in Washington as having "berries of delicious taste, sweet, slightly acid and of pronounced flavor." This plant was pollinated with Rubel pollen in 1915, and the Scammell blueberry was one of the resulting seedlings. In the field the original bush of Scammell bore berries up to a diameter of 20.5 mm. On budded plants in the greenhouse in Washington they reached more than 22 mm. The berries have a medium blue color, firm texture, and a small scar, and the calyx is almost wanting. The leaves are smaller than on most varieties of highbush ancestry, commonly 1½ to 2 inches in length and five-eighths to three-quarters of an inch in width. The berries are sweet, subacid, and have a high degree of flavor. They ripen in late midseason. Among New Jersey growers there has been little planting of this variety, apparently from doubt regarding its vegetative vigor. In North Carolina, however, at the Double Trouble Company's blueberry plantation near Magnolia, it is regarded as one of their best varieties.

Stanley

The Stanley resulted from a cross between the Katharine blueberry and the wild Rubel bush, made in 1921. By many persons Stanley is considered the most delicious of all blueberries. The original bush bore berries a little less than 18 mm in diameter. From the first its berries were recognized as of especially delicious flavor. It is named for my son, Stanley, on whose blueberry plantation at New Lisbon, N. J., this variety was first shown to be capable of producing good yields of berries of large size. Its berries often exceed 19 mm in diameter and sometimes 20 mm. In one instance a Stanley berry reached a diameter of 21 mm and in another instance 22 mm. The Stanley blueberry is a late midseason variety.

Redskin

The Redskin blueberry is an albino, a second-generation hybrid between the wild highbush blueberry Brooks and the wild lowbush blueberry Russell. The original Redskin plant came from a pollination made in 1913. Albino blueberries become red on the side exposed to the sun. In the Redskin blueberry the red is almost that of old mahogany, with only a trace of bloom. The berry sometimes exceeds 16 mm in diameter, and the flavor is good. The berry ripens early in the season. This variety and the next, Catawba, were given names in 1932 because as red-cheeked albinos they are horticultural curiosities. The fair size and good flavor of their berries make them desirable additions to a collection of blueberry varieties for a home garden. It

is doubtful whether any albino blueberry will ever acquire importance as a market fruit. The white color of the shaded half of the Redskin berry gives the fruit a mottled appearance after picking, and on any slight bruise the injured portion of the flesh turns to a dried-apple color, both of these features making the fruit uninviting to a purchaser. The leaves of Redskin are finely toothed. This variety should be pruned at the end of the growing season by the removal of all the stems that fruited in the preceding summer, only the season's sprouts being left. When so pruned, Redskin hardly reaches a height of 2 feet. This low stature, which allows the plants to be kept covered with snow very easily during the bitter cold of a northern midwinter, suggests Redskin as a desirable variety in places so far north that other and taller varieties project through the snow and lose their fruit buds by winter-killing.

Catawba

The Catawba blueberry is an albino which was bred from the same grandparents and the same parents as Redskin, and in the same year. The berries of Catawba are not so large as those of Redskin, nor is their flavor quite so good. They have more bloom, and the red of the berry is therefore paler than in redskin, more like the color of the Catawba grape, a resemblance that suggested the varietal name. The leaves of the Catawba are finely toothed, and the plants reach a height of about 4 feet.

Wareham

In the autumn of 1916 some 300 pedigreed but untested blueberry seedlings were sent to the cranberry substation of the Massachusetts Agricultural Experiment Station, East Wareham, Mass., to be brought into fruit by H. J. Franklin, in charge of the cranberry substation. Among these seedlings was one that, after several years of observation, Professor Franklin thought was of sufficient merit to be named and distributed. In accordance with his wish it was named Wareham. The parents of the Wareham blueberry were the wild New Jersey highbush blueberry Rubel and another wild New Jersey highbush blueberry named Harding, after its discoverer, Ralph Harding. The cross-pollination was made in 1915. The original bush of the Wareham blueberry, in the late summer of 1931, had a breadth of 9 by 9 feet and a height of 6 feet. It was vigorous and had produced 8 quarts of berries that season. It differed from most other tall varieties of blueberries improved by breeding in having serrate leaves, like its Harding parent. When I saw the bush again, on July 28, 1933, its berries had not yet been picked. Several were over 19 mm in diameter, some of them nearly 20 mm. Wareham is a late-season variety, its berries maturing at about the same time as Jersey. Until they are dead ripe they are a little too acid for the taste of most persons. When fully ripe they are sweet-subacid and of good flavor.

Weymouth

The Weymouth is named for the cranberry and blueberry plantation of Weymouth, at which most of the Department's testing of new pedigreed blueberry seedlings has been conducted since 1929, between Hammonton and Mays Landing, N. J. It is near Weymouth Furnace, long ago abandoned, at which cannon and cannonballs were

made from bog iron ore during the War of 1812. The Weymouth blueberry is a cross between the two early varieties June and Cabot. The pollination was made in 1928. Although the earliness of Weymouth is not yet satisfactorily proved from commercial field experience, the original bush bore berries that reached nearly 22 mm in diameter and ripened much earlier than Cabot. The berries have only a moderate degree of acidity in the early stage of their ripening, and they are sweet, subacid, and delicious when they are first picked. They lose much of their taste if they are allowed to become overripe.

GM37

There is one seedling blueberry that, although barred from commercial culture because its berries are deficient in flavor, has other such desirable qualities, including the extraordinary size of its fruit, that acquaintance with this unnamed bush ought to be shared with the public. It is known in our records as GM37. It is a cross between Jersey and Pioneer, and therefore has four wild highbush ancestors, Grover and Rubel, the parents of Jersey, and Brooks and Sooy, the parents of Pioneer. The pollination from which GM37 came was made in 1925. The original bush produced berries in 1928 over 20 mm in diameter, in 1929 over 21 mm, and in 1930 nearly 23 mm. In 1933 a budded bush of GM37, hand-pollinated and screened, in a New Jersey blueberry plantation, produced berries up to 25.9 mm, a little over an inch, in diameter. (An inch is 25.4 mm.) A cluster of berries from this bush is illustrated, natural size, in figure 4. The reader should bear in mind that this is the largest blueberry ever produced, but it lacks the flavor required to warrant making it a named variety. For breeding purposes, however, GM37 has great value, as will be evident from what is said under the next variety, Dixi.

Dixi [4]

The unnamed blueberry GM37 lacked only flavor to make it a valuable variety. In 1930 it was cross-pollinated with the Stanley blueberry, the most delicious of all varieties. Among the progeny was a bush that attracted attention first in 1935 and again in 1936. Its berries are sweet-subacid and delicious. On July 9, 1935, the largest berry was over 21 mm in diameter, and on July 24 of that year over 23 mm. On July 24, 1936, the largest berry reached 24 mm. If the season of 1936 had been a favorable one for the development of large individual blueberries, I am confident that the berries on this plant would have reached a diameter of more than an inch. There is now only a single bush of this variety. It will be several years before it can be propagated for a thorough field test of its qualities. Nevertheless, there are circumstances that seem to make it desirable to give a name to this variety at this time. Toward the end of the present fiscal year I terminate my connection with the Department of Agriculture after 49 years of botanical research. It was the custom of Linnaeus and other scientific men of his time, when a

[4] Blueberry growers should be careful not to misspell the name of the Dixi blueberry, for the wrong spelling "Dixie" may give the erroneous impression that this variety is especially adapted to cultivation in the South. The ancestors of the Dixi blueberry were northern plants, and although the variety may be of value as far south as North Carolina, there is every reason to expect that it will not thrive in the Gulf States.

public address was given in Latin, to end the address with a Latin word that meant "I have spoken," "I have said what I have to say," or "I am through." Therefore, with orthographic apologies to the southern half of the United States, I name this blueberry and end this paper with that Latin word—*Dixi*

Figure 4.—A cluster of the largest blueberries thus far grown. (Natural size.) The largest berry on this bush was 25.9 mm (a little more than an inch) in diameter. This bush, known in our records as GM37, was not made a named variety because its berries were not up to our standard of flavor. It has been cross-bred, however, with the most delicious variety of blueberry, Stanley. Among the off-spring is the large and delicious blueberry described in this paper as Dixi, which already, as a young plant, has produced berries nearly as large as those shown in this illustration.

PROGRESS IN APPLE IMPROVEMENT

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THE apple we have today is far removed from the "gift of the gods" which prehistoric man found in roaming the woods of western Asia and temperate Europe. We can judge that apple only by the wild apples that grow today in the area between the Caspian Sea and Europe, which is believed to be the original habitat of the apple. These apples are generally only 1 to 2 inches in diameter, are acid and astringent, and are far inferior to the choice modern horticultural varieties.

The improvement of the apple through the selection of the best types of the wild seedlings goes far back to the very beginning of history. Methods of budding and grafting fruits were known more than 2,000 years ago. According to Unger, Cato (third century, B. C.) knew seven different apple varieties. Pliny (first century, A. D.) knew 36 different kinds. By the time the first settlers from Europe were coming to the shores of North America, hundreds of apple varieties had been named in European countries.

The superior varieties grown in Europe in the seventeenth century had, so far as is known, all developed as chance seedlings, but gardeners had selected the best of the seedling trees and propagated them vegetatively.

The early American settlers, particularly those from the temperate portions of Europe, who came to the eastern coast of North America, brought with them seeds and in some cases grafted trees of European varieties. Within a few years after the first settlements were made in the temperate portions of North America, bearing apple trees were reported.

From this start, apple trees were rapidly disseminated. The apple was apparently carried by Indians, traders, and missionaries into the wilderness far beyond the white settlements. In the early writings frequent mention is made of Indian villages with apple and peach

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[1] This article is made possible only through the cooperation of many workers on apple breeding in both the United States and Europe. Reports on which portions of this discussion are based have been received from the following State agricultural experiment station workers: Leif Verner, Idaho; M. J. Dorsey, Illinois; J. L. Lantz, Iowa; R. M. Bailey, Maine; A. L. Schrader, Maryland; J. K. Shaw, Massachusetts; W. H. Alderman, Minnesota; Paul H. Shepard, Missouri; State Fruit Experiment Station; A. E. Murneek, Missouri; Richard Wellington and G. H. Howe, New York (State) Station; F. S. Howlett and C. W. Ellenwood, Ohio; N. E. Hansen, South Dakota; Fred W. HofMann, Virginia; also from W. P. Baird, U. S. Northern Great Plains Field Station, Mandan, N. Dak ; C. P. Close, U. S. Department of Agriculture, Washington, D. C.; T. F Ritchie, acting Dominion horticulturist, Central Experimental Farm, Ottawa, Canada; Sir Daniel Hall, director, John Innes Horticultural Institution, Merton, England; Carl G. Dahl, Lantbruks, Mojeri-och Trädgårdsinstitut, Alnarp, Sweden; Ing. Fr. Landovský, State Institute for Horticultural Research, Průhonice, Czechoslovakia; Prof. Dr. Rudorf, Kaiser Wilhelm Institut für Zuchtungsforschung, Müncheberg, Germany; and H. Wenholz, Department of Agriculture, Sydney, New South Wales, Australia.

orchards adjacent to them; apparently the Indians were an important factor in the early dissemination of these fruits. All the Indian orchards consisted, of course, of seedling trees. Since the apple does not come true from seed, wide variations in size, color, and quality of fruit and season of ripening undoubtedly occurred in these early orchards. As the country became more settled, farmers and gardeners were interested in growing the best of these seedlings rather than in planting a miscellaneous assortment that could be secured from seed.

It is uncertain just when the first grafting of apple varieties was practiced in the United States. Taylor (*15, pp. 308–309*) [2] says:

> Certain it is that in 1647 the apple is recorded as grafted upon wild stocks in Virginia, while in 1686 William Fitzhugh, in describing his own plantation, mentions "a large orchard of about 2,500 apple trees, most grafted, well fenced with a locust fence." * * * Frequent importations of seeds, scions, and grafted trees, together with propagation from those already noticed, both by seeds and grafts, brought the orchards of New England up to such point that Dudley, in 1726, stated in a paper in the Philosophical Transactions, "our Apples are without doubt as good as those of England, and much fairer to look to, and so are the Pears * * * Our People of late years, have run so much upon Orchards, that in a village near Boston, consisting of about forty Families, they made near ten Thousand Barrels [of cider]."

[2] Italic numbers in parentheses refer to Selected References to Literature, p. 601.

APPLE *breeding is a task that requires not only great patience but ability to look well into the future. In most sections of the United States at least 10 to 15 years are required to grow an apple from seed to bearing age and to obtain an accurate evaluation of it. To propagate and test a promising kind will require an additional 10 to 12 years. Therefore not less than 25 years are usually required from the time a cross is made until the progeny of that cross can be fully evaluated. Additional years must then elapse before commercial orchards come into fruiting. Thus it usually takes from 30 to 40 years between the planting of the original seed and the production of commercial crops of even a very superior apple. Apples originating from the earliest breeding investigations in the United States, begun as far back as 1880, are just now coming into prominence; those from the breeding work of 20 or 25 years ago are not yet fully tested. It is easy to see, then, why few of our popular commercial varieties have as yet resulted from modern breeding work. However, there is every prospect that varieties superior to those now in use will result from the many thousands of hybrid seedlings now under test at various research centers.*

As settlements spread westward to the Mississippi Valley and on to the Pacific, apple planting kept pace. An eccentric missionary, John Chapman, known as "Johnny Appleseed", roamed the frontier settlements of Ohio and Indiana in the early nineteenth century, planting apple seed and starting orchards wherever he went and encouraging others to do the same. He lived to see bearing trees throughout the area. Thus the apple became more or less naturalized throughout the temperate part of North America.

The apple varieties grown here today are quite largely those that have been developed from the seedling trees that happened to be superior. Only a few of our important commercial varieties have been imported from Europe. During the past century the primary emphasis in the United States has been on varieties with superior dessert and cooking quality, along with good size, a range of ripening from midsummer to late fall, and a storage quality that will carry the fruit through the winter months. Perhaps the greater emphasis in Europe on the use of apples for cider making is partially responsible for the smaller number of really high-quality dessert apples selected there. Table 1, in the appendix, indicates the source of leading American varieties of apples so far as it is known.

Few of the apples that have reached commercial promise to date have been produced as a result of systematic hybridization. The reason for this is readily apparent when certain of the factors involved in apple breeding are considered. Practically no systematic work was started in the United States prior to 1880, and little was carried on prior to 1895. In most sections of the United States at least 10 to 15 years are required to grow an apple tree from seed to bearing age and to give an accurate evaluation of it. To propagate and test a promising kind will require an additional 10 to 12 years. Therefore not less than 25 years is usually required from the time a cross is made until the progeny of that cross can be accurately evaluated. Additional years must then elapse before commercial orchards come into fruiting. Thus from 30 to 40 years will usually elapse between the planting of the original seed and the production of commercial crops of even a very superior apple. Apples originating from the earlier breeding investigations are just now coming into commercial prominence. Since much of the breeding work has been conducted during the last 20 or 25 years, sufficient time has not yet elapsed to give a full evaluation of the offspring of the crosses made.

THE RAW MATERIALS OF THE APPLE BREEDER

The apple belongs to the great family of plants termed by botanists the Rosaceae, or rose family. This family is very large and includes many tree fruits of the Temperate Zone, such as plums and prunes, peaches, cherries, apricots, and pears, as well as strawberries, blackberries, and many other forms of cultivated and wild plants. Apples and pears belong to the pome fruit subfamily Pomoideae, which includes, in addition to these fruits, the hawthorns, cotoneasters, quinces, medlars, mountain-ash, and a number of additional related forms. All of the plants in this subfamily are characterized by having the seeds borne in a fleshy covering and having two to five carpels, or seed cavities, in each fruit. Within the Pomoideae the genus *Malus*,

comprising the apples, makes up one important group. Many botanists have included the apple in the pear genus, *Pyrus*. The fruits of these two groups are distinguished by the fact that the pears contain grit cells, while the flesh of the apple is free of grit cells. There are also other distinctive differences in the structure of certain flower parts.

The various species that make up the genus *Malus* can in most cases be hybridized rather readily. Species of *Malus* apparently do not hybridize readily with species of *Pyrus* or with those of other genera in the Pomoideae. No such crosses have been reported, although there has been ample opportunity for them to occur naturally in view of the wide distribution and adjacent plantings of many members of these genera.

There is some difference of opinion among botanists as to whether one or more than one species originally entered into the parentage of our cultivated apple. The wide diversity of existing forms has led some students to believe that several species were involved originally. However, this diversity might well be expected in a fruit crop selected and cultivated for thousands of years and propagated largely by vegetative means. Every interesting variation occurring in seedlings could thus be preserved.

In addition to the cultivated apple, Rehder, in his Manual of Cultivated Trees and Shrubs, lists 24 species of apples or crab apples, native mainly in China, Siberia, Japan, and the United States. Bailey in his Manual of Cultivated Plants makes a somewhat different division, listing 25 species of *Malus*. Knowledge of the close relatives that might be expected to hybridize readily with the cultivated apple is of much interest from the breeding standpoint.

While these species represent basic raw material available to the apple breeder, for most purposes it is not desirable to use the original types in breeding work. The selection of superior varieties through the centuries has given us breeding material that is far more promising than the parent species for the development of superior new kinds by hybridization. Only when special characters, such as extreme hardiness, are needed does it seem more desirable to use original species material. For the production of crab apple types and for ornamental purposes, however, these species are of outstanding value.

OBJECTIVES IN AMERICAN APPLE BREEDING

Objectives in the apple-breeding work vary, of course, in different sections. Throughout most of the apple belt in the United States increased winter hardiness is highly desirable, and in the colder sections, including the northern Great Plains area and northern New England, it is the all-important factor in apple production. A few varieties such as McIntosh, Wealthy, Oldenburg, and Yellow Transparent are sufficiently hardy for all but the northernmost part of the Plains region. Many important varieties, including Baldwin, Stayman Winesap, Winesap, Grimes Golden, Rome Beauty, Yellow Newtown, and Jonathan, may be severely injured or trees may be killed during severe winters in many sections of the country. Increased hardiness must continually be sought in the apple-breeding program for all but possibly the southeastern districts.

The second most important objective is greater disease resistance. The five diseases that cause the greatest loss of apples in the United States are scab, blotch, bitter rot, fire blight, and apple cedar rust. There are wide degrees of susceptibility to all of these diseases. No commercial variety is immune from scab. However, McIntosh, Delicious, Stayman Winesap, and Rome Beauty are far more subject to the disease than are Grimes Golden, York Imperial, Baldwin, or Jonathan. Similarly, Golden Delicious, Yellow Newtown, Grimes Golden, and Jonathan are extremely subject to bitter rot, and for this reason they are of doubtful value for planting in the far southeastern districts. On the other hand, Winesap, Baldwin, Delicious, Rome Beauty, Stayman Winesap, and York Imperial are relatively resistant to this disease.

Varieties very susceptible to blotch include Ben Davis, McIntosh, Northwestern Greening, and Oldenburg, while a list of relatively resistant varieties includes Delicious, Grimes Golden, Jonathan, Stayman Winesap, and York Imperial.

Baldwin and Delicious are highly resistant to apple cedar rust, while Jonathan, Rome Beauty, Wealthy, and York Imperial are quite susceptible. Seedlings of resistant parents show a high degree of resistance to this disease, while seedlings of susceptible parents are highly susceptible.

Fire blight is a serious orchard disease of Yellow Transparent, Jonathan, Wealthy, York Imperial, and a number of other varieties. On the other hand, Delicious, Ben Davis, and the Winesap family of varieties are resistant. We know that seedlings of Yellow Transparent tend to be susceptible, but we have little information as to how the characters of susceptibility or resistance to fire blight or other diseases behave in hybridization.

Susceptibility to spray injury also is an important character from the standpoint of evaluating a variety for commercial use. Golden Delicious and Ben Davis are particularly susceptible, while many varieties, including Delicious, McIntosh, Rhode Island Greening, Rome Beauty, Stayman Winesap, and others, show little injury.

The securing of new varieties fairly resistant to all of these diseases and to spray injury is a distinct possibility. It should be a primary objective in breeding, and all new selections should be studied from the standpoint of disease susceptibility.

The third objective, important in many parts of the United States, is the securing of late-blooming varieties that will have a greater possibility of escaping spring frosts and freezes. In most apple sections spring frosts or freezes are likely to reduce the apple crop greatly in certain years. In some sections this may run as high as 2 years in 5, in other sections perhaps not over 1 year in 10. Varieties blooming a week to 10 days later than standard types would have an increasingly better chance to escape such losses. This is particularly important in some of the midwestern areas. The late-blooming character is present in Rome Beauty, Mother, Ralls, and some other varieties, and through the use of such varieties in breeding, late-blooming trees can be obtained.

A fourth objective is the securing of varieties having highly developed, rich flavor combined with desirable tree characters.

Among highly flavored varieties are Delicious, Golden Delicious, Esopus Spitzenburg, Jonathan, Grimes Golden, and McIntosh. Many of these have horticultural weaknesses such as lack of hardiness, disease susceptibility, insufficient tree vigor, and susceptibility to spray injury.

It is desirable to obtain high-quality, attractively colored varieties that will be available throughout the year through the use of cold storage. Improvement in color in our present varieties is being accomplished by selection of attractive, highly colored bud mutations. On the average our long-keeping varieties are inferior in quality to those that are available earlier in the season, such as McIntosh, Grimes Golden, and Jonathan.

Another important objective is the development of varieties adapted to the far South. At present there are no satisfactory varieties for the region within 200 miles of the Gulf of Mexico. Native crab apples might be of value for hybridizing to produce varieties adapted to that region. No active work of this kind is under way, but there is a real need for it. Until apples can be grown locally, many people in that region will never have an adequate supply of the fruit.

The relative importance of these different objectives varies in different regions. In the Southeastern States disease resistance is of major importance. In the northern Plains area winter hardiness becomes the most important single objective. In the Missouri and Ohio Valleys, late blooming to escape the hazards of spring frost assumes major importance. Throughout all of the regions a succession of high-quality varieties available for use throughout the year is highly desirable.

METHODS OF IMPROVEMENT BY SELECTION OF BUD MUTATIONS

OCCASIONALLY cell division in the vegetative tissues fails to reproduce a new cell exactly like the parent. The result is an occasional branch or bud that varies in some respect from the parent tree on which it is borne. Such a mutant branch or bud normally reproduces true when propagated vegetatively, provided the variation is a true mutation and has not been caused by environmental conditions.

The fact that such bud or branch mutations occasionally occur has long been known to plant propagators. It is only in recent years, however, that the importance of these variations, from the standpoint of improving our fruit varieties, has been fully appreciated.

During the past decade an intensive search of American apple orchards has been conducted to locate such mutations as may be of value. Since red-colored apples command a considerable premium on the American markets, mutations carrying a greater amount of red color have been particularly sought. How successful the search has been is indicated by the fact that we now have more than 30 red strains of the Delicious variety. Many of these red strains, however, may prove to be so similar as to be practically indistinguishable. More than 15 red strains of Rome Beauty are known, 20 strains of Winesap, 8 strains of Stayman Winesap, and several strains of McIntosh, York Imperial, Jonathan, and other leading varieties. At the present time, strains believed to color earlier or to have better color are in existence

for practically all of the leading red or blushed apple varieties. In several varieties, namely, Delicious, Rome Beauty, Winesap, Jonathan, and Stayman Winesap, new commercial plantings are largely of the improved strains rather than the standard varietal forms.

It has been assumed by many nurserymen and growers that in general such mutations vary from the parent in only one character. This is not necessarily true. Variations in season of ripening, fruit size, storage quality, dessert quality, or productiveness may accompany color variations. Therefore the various bud mutations should be thoroughly tested before they are widely propagated commercially.

In addition to mutations affecting color, a few have been found that involve season of maturity, size, shape, and flavor of fruit. It is of course obvious that variations in flavor, storage quality, or productiveness are less likely to be located than are variations of color or season of maturity, which are very conspicuous when the fruit is still on the tree.

A search for bud mutations is especially likely to lead to rapid results in the improvement of horticultural varieties. Generally these mutations mean only a slight difference in varieties that have already proved themselves excellent from a commercial standpoint. For example, the Winesap apple is already established as a leading commercial variety. Its greatest weakness is its tendency to rather small fruit size and lack of tree vigor under all but the best soil conditions. Its growing season is too long to permit proper development of the fruit in northern districts. Thus, bud mutations of Winesap that would give an earlier ripening apple would extend the range northward. Similarly, a mutation showing larger size of fruit would be of much value. A search for such mutations should be continued in American orchards.

The process of selection, propagation, and testing of bud mutations perhaps offers a possibility for more rapid improvement of our present desirable varieties than does any other method of breeding. Possibly by bud selection we might find a later maturing McIntosh adapted for growing farther south than the present McIntosh belt, or an earlier maturing Stayman Winesap, Rome Beauty, or Winesap, which would mean better adaptation to northern sections. The fact that color can be improved by the use of such selections has already been amply demonstrated. The testing of bud mutations should be an integral part of the variety-improvement program in the years to come. For originating definitely new types of apples, however, or for the incorporation of new characters, such as greatly increased hardiness or vigor, hybridization appears to offer the greater possibilities.

HYBRIDIZATION OF APPLES. AND PEARS

There is no unusual difficulty in the technique of hybridizing apples and pears. Several steps of this technique are illustrated in figure 1. The flower parts of an apple or pear, in order, from the outside of the blossom to the center, are as follows: (1) The calyx, consisting of 5 sepals at the base of the blossom; (2), the corolla, made up of 5 white or pink petals; (3), the stamens or pollen-bearing organs, usually 20 in number, which are borne just inside the petals; (4), the pistil, the central organ that contains the seeds. In hybridizing most varieties

it is desirable to remove the pollen-bearing stamens from the flower before it opens. The best time to do this is at the so-called balloon stage, illustrated in figure 1, *A*, while the petals still form a complete covering over the inner flower parts. At that stage the stamens have not yet begun to shed pollen and there has previously been no opportunity for either self- or cross-pollination to occur.

Two methods may be employed in removing the pollen-bearing organs. In the method shown in the figure, the thumbnail or a small

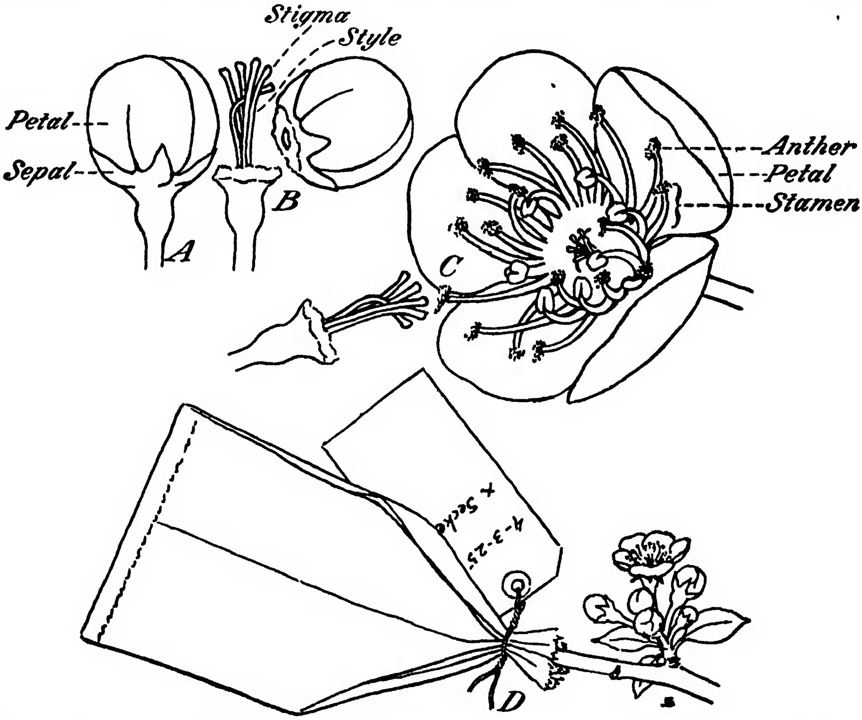

Figure 1.—**Steps in hybridization of apples and pears: *A*, Bud in proper stage for emasculation; *B*, after emasculation, showing petals, sepals, and stamens pinched off and removed; *C*, an open flower, showing the flower parts that are removed in emasculation; *D*, the method of protecting emasculated flowers from chance pollination.**

knife or a laboratory scalpel is used to make a cut just at the base of the sepals. The flower part is then bent sidewise, and the whole flower organ except the pistil can be torn loose, as shown in figure 1, *B*. If carefully done, this leaves the pistil, consisting of the ovary containing the seeds, with a cluster of styles and stigmas, as shown in *B*. The tearing loose of the flower parts may result in enough injury to reduce the set of fruit. In the second method, which is somewhat slower but less likely to cause injury, the petals are pulled loose at the stage shown in *A*, and the anthers are picked out of the blossom with an instrument; an ordinary comb is satisfactory.

If the flowers are within a day or two of opening when emasculated, it is satisfactory to apply the pollen of the selected male parent at the

time the emasculation is done; or the application of pollen may be postponed for a day or two. The pollen should be applied, however, before the stigmas begin to turn brown. The emasculated blossoms must be protected from chance pollination for several days. A satisfactory method is shown in figure 1, *D*.

A higher percentage of set of fruit will usually result if not more than two blossoms are emasculated and pollinated in a cluster. The remaining blossoms should, of course, be picked off at the time the emasculating is done.

Handling the Pollen

To secure pollen, buds in the stage shown in figure 1, *A*, are picked and the anthers combed out of them as described above. If these anthers are held in a moderately warm, dry place they will ripen rather rapidly and begin to shed pollen within 24 to 48 hours.

Sometimes branches of the desired pollen parent are brought into a room or a greenhouse before the blossoms open, set in water, and allowed to bloom protected from insects. The pollen is removed from the open flowers when it is ripe.

Pollen is usually applied to the stigmas of the emasculated blossoms with a fine camel's-hair brush, which may be sterilized between pollinations by washing in alcohol or immersing for several seconds in boiling water. After the pollen has been applied, the emasculated blossoms should again be protected (fig. 2). When conditions are favorable, from 30 to 50 percent of the emasculated blossoms should set fruit. After the stigmas have turned completely brown the protecting bags may be removed and labels designating the cross should be carefully adjusted. The fruit may be harvested when slightly immature to prevent undue loss from dropping. Germination of the seed is not affected by such early harvesting.

Handling the Fruit and Seeds

Two or three alternative methods may be used for handling the fruit and seeds after harvest. Since apple and pear seeds must go through certain transformations, often described as "resting" or "after ripening," before they will germinate, the fruit may be placed in cold or cellar storage and held until spring. The seeds can then be removed and immediately planted in nursery rows. An alternative method of handling is to remove the seed from the fruit after harvest, place it in small labeled bags, and put these in cold storage over winter. It is necessary that the seed be sufficiently well dried and that it be stored in a sufficiently dry place to prevent it from molding, but excessive drying should be avoided. A third method is to stratify or bury the seed and carry it over winter outdoors. If facilities are available, the seed may be planted in flats in the greenhouse or in coldframes and the seedlings allowed to grow 3 or 4 inches high before being transplanted to nursery rows in the field, but this is not necessary.

After 2 years in the nursery row the apple seedlings may be transplanted to the orchard, sufficient space being allowed to permit the trees to come into fruit. Pear trees can be planted at somewhat closer distances in the orchard than apple trees; they will usually fruit satisfactorily if planted about 4 feet apart in the row, with the rows

Figure 2.—Cross-pollinated apple blossoms protected under glassine bags and labeled.

about 15 feet apart to facilitate cultivation and spraying. Apple trees should have at least 10 feet of space in the row, with rows 15 feet apart, if the fruiting value of the young trees is to be adequately determined.

To speed up the testing and at the same time conserve space, buds or grafts from young seedling trees may be put into older trees growing in

orchard form. Several buds or grafts may be put into an apple tree 4 to 6 years old. Usually it is preferable to have only seedlings of the same parentage worked on one orchard tree. If such a tree is maintained in good vigor and if the budding or grafting is satisfactorily accomplished, fruiting records should be obtained within 3 to 4 years from the date of budding or grafting. Usually budwood or scions from the seedlings can be obtained at the end of the first growing season. Thus, by this method, an indication of fruit value with apples or pears can be obtained in about 5 years from the time of making the cross. If the seedlings themselves are grown to fruiting age in the orchard, 8 to 10 years will usually be required. However, growing the seedling itself to fruiting permits a better evaluation of the tree from the standpoint of vigor, hardiness, disease resistance, and tree form.

In using the budding or grafting method, it is desirable to have trees that are not too old. Young orchard trees 4 to 5 years old are most nearly ideal from the standpoint of top-working, and they are small enough to facilitate the work of taking records on fruiting branches.

Several steps in apple breeding as carried on at the New York Agricultural Experiment Station at Geneva are illustrated in figures 3, 4, and 5.[3]

Significance of Unusual Chromosome Numbers

It is only within the last 10 years that we have had definite information on the chromosome numbers of the various apple varieties. This has clarified our understanding of the behavior of varieties, particularly from the standpoint of pollination and breeding. We now understand the reasons for the peculiar behavior of certain varieties long observed in the orchard.

Investigators have known for some years that certain varieties are poor pollinizers for others. They do not form much good pollen, most of the grains being abortive and failing to grow when put in a sugar solution suitable for pollen germination. Usually when these varieties are planted alone or in blocks with others of similar type, poor sets of fruit are secured. Among the varieties known as poor pollinizers are Stayman Winesap, Baldwin, Rhode Island Greening, Gravenstein, Arkansas (Black Twig), Tompkins King, Stark, and several less important ones.

These varieties have certain other characteristics in common also. All produce large-sized fruit, and all are vigorous growers and develop into large trees. Nursery investigations have indicated that as a rule seed produced by these varieties germinates poorly and the seedling trees are usually weak growers.

Our present knowledge of the number of chromosomes in apple varieties has been contributed by many investigators in many countries, including V. A. Rybin, in the Union of Soviet Socialist Republics; A. A. Moffett, M. B. Crane, W. J. C. Lawrence, and C. D. Darlington, in England; J. S. Shoemaker and B. R. Nebel, in the United States; F. Kobel, in Germany; O. Heilborn, in Sweden; and others. These workers have shown that most of the cultivated varieties of apples have 34 chromosomes (17 pairs) in the vegetative or somatic tissues, and 17 (one member of each pair) in the germ cells. These varieties

[3] From photographs furnished by the station.

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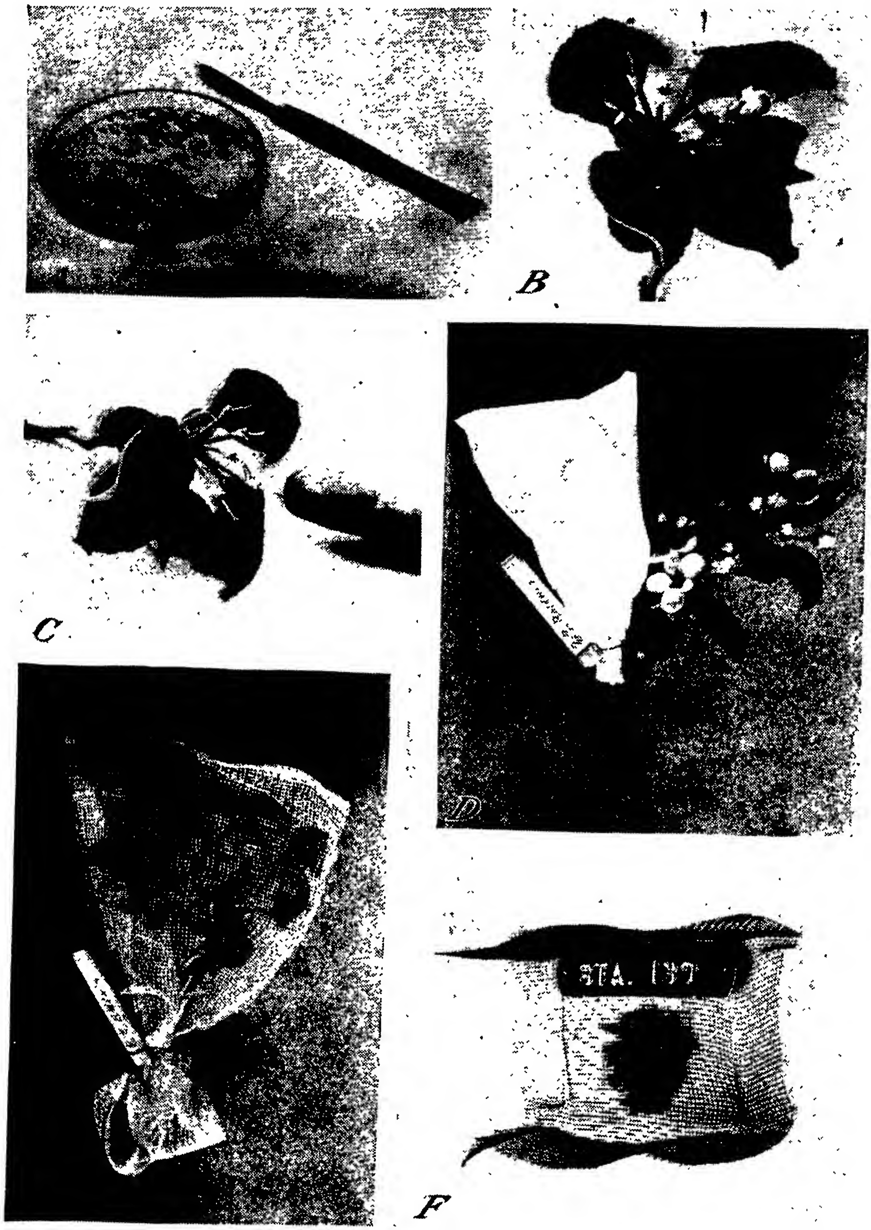

Figure 3.—Steps in apple breeding: *A*, Collecting pollen from unopened clusters; *B*, blossoms emasculated and ready for the application of pollen (note that the pollen-bearing organs have been removed); *C*, applying pollen to the pistils of the emasculated flowers; *D*, pollinated flowers protected from chance pollination by covering with paper bags; *E*, mesh bags used to protect the fruit that has set; *F*, seeds resulting from controlled pollination, protected by mouse-proof screen for stratifying in soil.

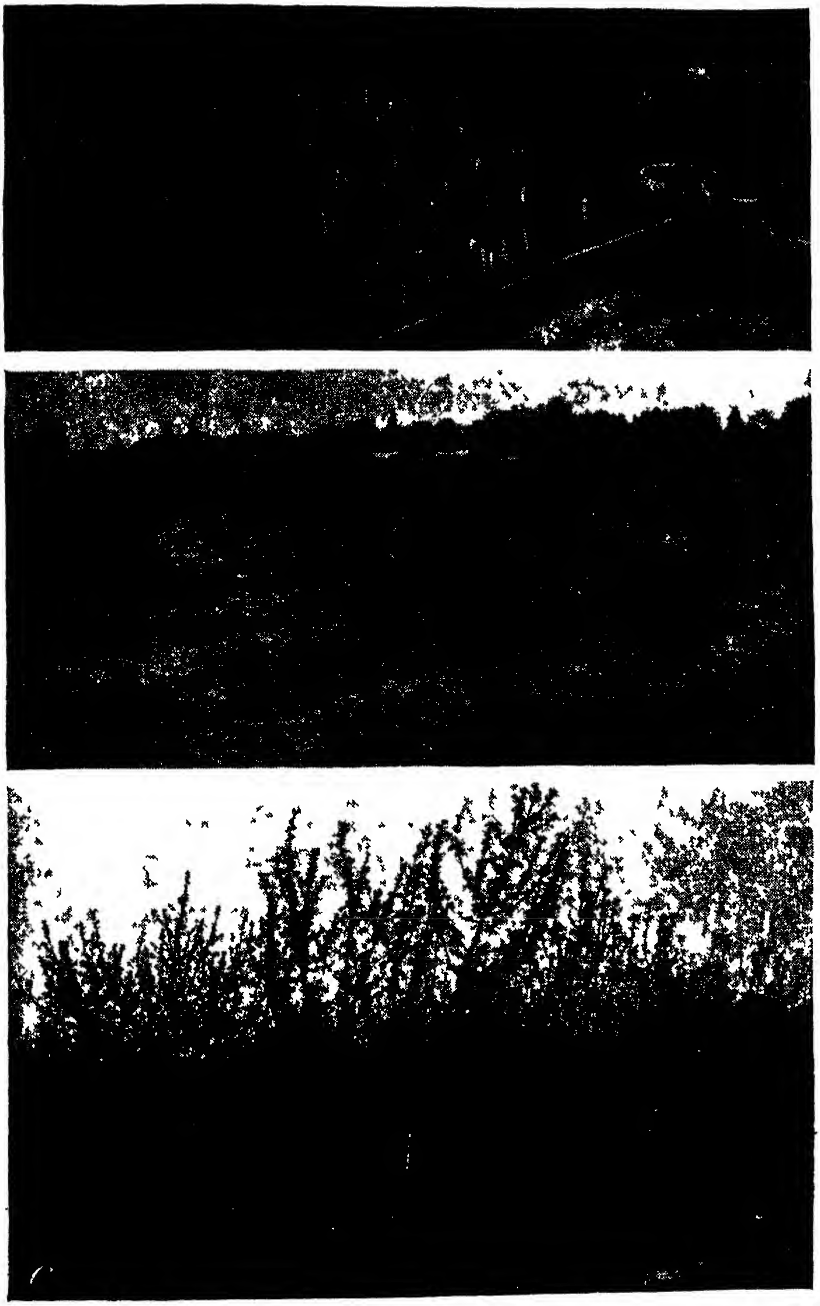

Figure 4.—Steps in apple breeding; *A*, Young seedling trees grown in flats prior to setting in the field; *B*, planting of young hybrid trees in orchard form; *C*, a hybrid orchard in fruiting. At this stage undesirable seedlings can be eliminated.

with 34 diploid chromosomes as a rule produce fertile pollen and they are generally classed as good pollinizers for other varieties. The trees vary in vigor from low to moderately high, and fruit size varies from small to large.

The peculiarity of the second group of varieties, described above as being partially or in some cases almost entirely pollen-sterile and

Figure 5.—Second tests of promising hybrid selections. The tree in the foreground is Early McIntosh.

producing large fruit and large vigorous trees, is that they have 51 chromosomes instead of 34 in the somatic tissues. They are termed triploids,[4] since the chromosome number in the vegetative tissue is three times that of the usual reproductive cells of apples, instead of twice, as in the diploids.

[4] This is discussed by A. F. Blakeslee in his article in this Yearbook.

The question arises, How have these triploid varieties developed? Normally the cells of the vegetative tissue have only twice as many chromosomes as the reproductive cells. How can we account for the considerable number of apple varieties that carry three times this basic chromosome number?

It is not known definitely how the triploid forms developed. At long intervals, the frequency varying with different species, a germ cell in either the male or the female organs may be developed with an extra set of chromosomes. Experimentally, cells are occasionally formed with double the normal number of chromosomes as a result of subjecting them during the process of germ-cell formation to unusual environmental conditions, such as high or low temperatures. It may be deduced, therefore, that at rare intervals under natural conditions pollen grains or egg cells are formed that carry 34 rather than 17 chromosomes in the reproductive cells.

Now if an egg cell carrying 34 chromosomes is fertilized by a sperm carrying 17 chromosomes, the resulting fertilized egg will have 51 chromosomes. It will develop into an embryo and ultimately into a plant carrying 51 chromosomes in its vegetative tissues. If such a tree is propagated vegetatively, the result is a horticultural variety with 51 chromosomes instead of the normal 34.

Approximately one-fourth of all commercial apple varieties are these triploid or 51-chromosome forms. Yet it is probable that such forms are rarely produced among seedling apple trees. For example, in all of the controlled breeding work that has been done in the United States, involving crosses of diploid × diploid, diploid × triploid, triploid × diploid, and triploid × triploid, no seedling of merit known to be a triploid has been produced. It is apparent, therefore, that in nature triploid forms are produced only rarely as compared to diploids.

How, then, can we account for the fact that at least a fourth of our important varieties are triploids? This is possible only if we assume that the triploids have characteristics that make them of unusual value as commercial varieties, so that an unusually high proportion of the triploid forms have been selected and propagated as varieties. It is probable that in the United States in the last 250 years more than 200,000,000 apple trees of seedling origin have grown and fruited. Even if only 1 in 50,000 of these was a triploid, it would mean that several thousand triploid trees have grown in the United States some time during the past two and a half centuries. If these trees on the average had certain superior characteristics as compared with the hundreds of millions of diploid trees, they could easily have become the source of a relatively large number of improved varieties. Some of their characteristics of unusual value from a commercial standpoint have already been enumerated, namely, large size of fruit and vigorous growth and large size of trees. Heilborn (*9*) has also pointed out that most of the triploid varieties grown in Europe have relatively long storage quality. This does not apply to all of the American triploid varieties, but many of them are firm-fleshed apples of good storage quality. Thus it seems probable that from the mass of seedling material available in the United States and Europe a relatively high proportion of the rare triploids has been selected and a relatively small proportion of the more common diploids.

Can We Breed for Triploid Varieties?

These points of superiority of the triploid varieties would indicate that attempts should be made to secure triploids in breeding. It is true that a large portion of the seedlings produced in breeding work tend to run to medium or small fruit size. This tendency could undoubtedly be corrected if triploid varieties could be obtained at will. Unfortunately, however, this cannot be done.

As explained above, crossing of diploid × diploid varieties normally gives only diploids. What occurs when we cross diploids × triploids or triploids × triploids?

The triploid somatic or vegetative cells contain 51 chromosomes—34 obtained from one parent germ cell and 17 from the other. In the pairing of the chromosomes, which takes place prior to the formation of germ cells, 34 will pair normally into 17 pairs. But the remaining 17 of the 51 chromosomes are not arranged in any special order, and they are unable to pair among themselves. After pairing, the chromosomes again divide, half going to one pole of the nucleus and half to the other pole. But the 17 unpaired chromosomes cannot do this in an orderly fashion. Some of them go to one pole and some to the other at random. Thus, when the cell finally splits in half to form two germ cells, we find that each of these contains 17 chromosomes from the original pairs and an indefinite number of other chromosomes from those that had not paired. This indefinite number varies all the way from none at all to the whole 17 unpaired chromosomes. Such a germ cell may have any number of chromosomes from 17 to 34.

The great majority of these germ cells with an irregular chromosome number are sterile. The addition of chromosomes above the normal number but less than double the number seems to result in sterility to a large extent throughout the plant kingdom. In apples, however, some viable pollen grains are found in most of the triploid forms, and in most varieties enough of the egg cells are sufficiently fertile to give a satisfactory fruit set, particularly if they are pollinated with diploid pollen.

However, when the egg cell containing 17 to 34 chromosomes is fertilized with a nucleus from diploid pollen containing 17 chromosomes, we usually will have neither diploid nor triploid offspring. The number will vary from 34 to 51, that is, 17 from the pollen cell plus 17 to 34 from the egg cell. These are called aneuploids, and the seeds generally germinate poorly. Those that do grow are likely to produce weak seedlings, though occasionally they are fairly vigorous. It is of interest to note, however, that of the varieties that have been introduced as a result of breeding work in the United States to date, none has a parent of known triploid constitution. This is in line with cytological studies on many species of plants, which indicate the slight probability of obtaining promising varieties when one or both of the parents are triploids.

Triploids crossed with triploids also are likely to give aneuploid progeny. Here the possible number of chromosomes will range from 34 to 68 and may be expressed numerically by the formula $[17+(0\text{ to }17)]+[17+(0\text{ to }17)]$. Such triploid × triploid progeny are likely to be weak vegetatively if they grow at all.

In order to obtain triploids at will in breeding, it is necessary to have a tetraploid parent (four times the basic number) to cross with a diploid. We do not now have any apple or pear varieties that are known to be tetraploids. There is a possibility that tetraploids resulting from chromosome doubling in some cell in the vegetative tissues originate at rare intervals as bud sports or somatic mutations in normal diploid varieties. One or two mutations that may be of this type have recently been found in pears, though their nature has not yet been definitely determined. If similar mutations can be found in apples, they will be of great interest from the breeding standpoint. Such bud sports will probably be characterized by giant fruits, since the character of giantism is often associated with chromosome doubling. Giant strains of apples, occurring as bud sports, should be carefully preserved until their character can be determined, even though the fruit itself may appear to be of no value.

Aside from diploid and triploid varieties, a word should be said as to the chromosome make-up of the genera *Malus* and *Pyrus*. These genera and other closely related forms stand out among the Rosaceae in having 17 chromosomes in the reduced phase (the reproductive cells), whereas the basic number in other genera of the family is mostly 7 and in a few 8 or 9. In *Malus* and *Pyrus* the 17 chromosomes are believed to represent multiplication from the simpler base of 7, 8, or 9, either by hybridization or by polyploid mutations. This complex chromosome constitution of apples and pears may account for the fact that there is such wide variation in selected varieties within these species, that mutations both in seed reproduction and vegetative tissues occur fairly frequently, and that most selected varieties are highly heterozygous, failing to reproduce seedlings closely resembling the parent.

INHERITANCE OF TREE AND FRUIT CHARACTERS

Most of our apple varieties are highly heterozygous, or mixed in their inheritance. This fact, coupled with the long time required to grow a generation, the impossibility of successfully selfing most varieties, and the relatively small populations that can be grown, makes the working out of inheritance factors difficult. The following summation is taken mainly from Wellington (*17*), Auchter (*2*), Lantz and Bole (*12*), and Crane and Lawrence (*6*).

Triploid × triploid or triploid × diploid varieties produce generally weak trees if seeds grow, because of aneuploid chromosome make-up.

Among diploid × diploid crosses, weak growth appears recessive to vigorous growth.

Tree shape—spreading, round, or upright—appears to be due to a number of genes. Forms of hybrids are usually intermediate between parents, with the progeny tending to be more nearly round than a strictly intermediate form would be.

Age of bearing is undoubtedly inherited, but simple segregations have not been obtained. Late-bearing and early-bearing parents tend to transmit these tendencies.

Susceptibility to apple cedar rust, to blight, and to scab appears to be inherited, but little is known of the segregations involved.

Date of fruit ripening follows parent behavior closely. Late-ripening parents give late-ripening progeny; early-ripening parents, early-ripening progeny; and early × late crosses usually ripen between the ripening dates of the two parents. In fruit size, large size seems dominant over small, but the factors are complex. Small crab apples crossed with apples give intermediate sizes. Most large apples carry some factors for small. To secure large size, cross large × large. Large × small fruit sizes yield progenies that are usually intermediate. Crane and Lawrence found the average of the progeny to be somewhat smaller than the average of the two parents.

Yellow or green skin color usually behaves as a recessive, though occasional red apples will appear in yellow × yellow hybrids. Apparently a number of factors are involved in color. Blush × blush parents may occasionally give deeper reds than either parent.

Flesh texture appears to follow parent type to a considerable degree, but some coarse-fleshed progeny are produced by tender-fleshed parents. Several factors appear to be involved in flesh texture, as well as in flesh color.

In flavor, sweet (lack of acidity) appears to be recessive. Some highly acid varieties, as Boiken, Oldenburg, and Montgomery, seem to be homozygous, or "pure" in their inheritance, for acidity. Mildly acid varieties give some sweet progeny and appear heterozygous for sweetness. Acid × acid gives a considerable proportion of progeny with acidity accentuated beyond either parent.

APPLE BREEDING IN THE UNITED STATES

A RELATIVELY large program of apple breeding is now under way in the United States, with active projects at 12 experiment stations and work at two points by the United States Department of Agriculture. The past and present workers in apple breeding are listed in the appendix. (See table 4.) In table 3 are summarized the crosses made at the stations that have fruited to date, together with the number of progeny from each cross considered to have horticultural promise, either as varieties or for further breeding work.

In the following pages, the work at the various stations is briefly summarized.

IDAHO

At the Idaho Agricultural Experiment Station, Moscow, breeding was begun in 1909 by C. C. Vincent, and since then 11,824 hybrid seedlings have been planted in orchard form . Results have indicated that the Jonathan, Wagener, and Esopus Spitzenburg varieties have tended to give highest dessert quality. Ben Davis crosses have the highest percentage of seedlings showing good keeping quality. No varieties have yet been introduced to the trade, but 101 selections have been made for detailed study.

ILLINOIS

Since the work was started at the Illinois Agricultural Experiment Station, Urbana, in 1908 by C. S. Crandall, approximately 15,000 trees have been fruited in the orchard, and detailed records have been made of the characteristics of the fruit produced. In the earlier work, a large number of crosses were made between cultivated varieties and

various species of crab apples. Later, the emphasis has shifted to hybridizing commercial varieties containing the qualities desired. The primary objective in the early breeding work was to secure data on genetic behavior of the apple. This is being continued, but greater emphasis is now placed on the securing of high dessert quality and good keeping quality in new varieties. At the present time, almost 3,000 seedlings representing high-quality parents are being grown. The principal varieties used in this later breeding work include Akin, Delicious, Jonathan, Golden Delicious, Maiden Blush, Fameuse, Winesap, Fanny, Grimes Golden, and Rome Beauty. In breeding for early apples of good quality, Yellow Transparent is being crossed with high-quality standard-season varieties.

From the seedlings that have fruited, 338 promising selections are being held for further observation as to their commercial value No varieties have been named.

Iowa

Apple-breeding work in Iowa was begun by C. G. Patten (fig. 6) at Charles City about 1867. Patten began as an independent fruit breeder but later received some financial assistance from the Iowa State Horticultural Society. From 1909 to 1914 the United States Department of Agriculture assisted in the work. In 1916 the State purchased the farm and fruit-breeding materials and the station was operated by the Iowa Agricultural Experiment Station until 1932. Patten introduced several varieties—Patten, Eastman, Brilliant, Silas Wilson, Iowa Beauty, and University. A number of selections from his work are still being used by the Iowa station.

Figure 6.—Charles G. Patten (1832–1921), a pioneer breeder of hardy apples, pears, and plums at Charles City, Iowa.

Work in fruit breeding and variety testing was begun at the Iowa Agricultural Experiment Station, Ames, about 1880, by J. L. Budd. The primary objective was to secure varieties of fairly good quality that would be hardy and productive under the severe winter conditions existing in Iowa. A large number of Russian varieties were introduced between 1880 and 1890 and tested at Ames. Most of these were not of desirable quality although many were extremely hardy. The inherent hardiness of this group of apples suggested their value for breeding. That they transmit their hardiness to their seedlings has been amply demonstrated by the work at the Iowa station since 1917. Budd grew seedlings of many open-pollinated fruits during the period from 1882 to 1905. Fruiting records were not made, and the results of this earlier work are not available. In general, results were

not sufficiently good to warrant continued work with open-pollinated seedlings.

The cross-breeding work in apples was initiated by S. A. Beach (fig. 7) in 1905, and large numbers of crosses were made between 1906 and 1910. Further breeding work was not attempted until the crosses were fruited. The seedlings began to fruit in 1916 and were described and the results tabulated by H. L. Lantz, T. J. Maney, and others, under the direction of Beach.

Figure 7.—Spencer Ambrose Beach (1862–1922). As head of the horticultural work at the New York (State) Agricultural Experiment Station from 1891 to 1905, and at the Iowa Agricultural Experiment Station from 1905 to 1922, he laid sure foundations for the splendid work of both stations in the breeding of fruit crops.

In an effort to bring the seedling trees into fruiting as early as possible, top-working was practiced, with three to five different seedlings worked on suitable stocks. While top-working was found to promote earlier bearing, several difficulties developed. Some scions failed to make satisfactory growth because they were too heavily shaded by more vigorous neighbors. Records were difficult to make because of confusion as to location of each graft on the tree. The growth habit of the tree could not be satisfactorily determined on top-worked material. In later work, therefore, the practice of top-working was discontinued. The varieties that have been introduced to date as a result of the breeding work at the Iowa station are listed in table 2 in the appendix.

After most of the crosses made by Beach had fruited, additional crossing was started and has been carried on with little interruption. At the present time, about 13,000 seedlings are being grown to fruiting from crosses made since 1917. A considerable number of these are now fruiting. A summary of the parentage of these seedlings is published in the Transactions of the Iowa State Horticultural Society, 1935.

Maine

Breeding work was begun at the Maine Agricultural Experiment Station, Orono, in 1911, but no records of the earlier work are available. Approximately 1,000 seedlings of crosses of McIntosh, Golden Delicious, Delicious, Northern Spy, Wealthy, and Cortland are now growing in nursery rows. Additional crosses involving the above varieties and Haralson and Scott Winter have been made during the past year. The objectives in this work are to secure hardy, high-quality varieties adapted to New England.

Chromosome counts have been made on several apple varieties. The following apparently are diploids: Ben Davis, Oldenburg, Early Harvest, Golden Delicious, LaRue, McIntosh, Milden, Northern Spy, Opalescent, Porter, Red Astrachan, Golden Russet, Chenango, Tolman Sweet, Wealthy, Wolf River, and Yellow Transparent. Varieties showing irregular chromosome numbers, probably triploids,

Figure 8.—The fruits of breeding: Apple orchards in the Shenandoah-Potomac Valley section.

include Baldwin, Gravenstein, Rhode Island Greening, Rolfe, and Stark.

Maryland

Breeding work at the University of Maryland, College Park, was started in 1906. The objective at first was to produce early-ripening red varieties of good quality. A total of 1,073 seedlings were grown prior to 1917. In this group of seedlings, 13 were selected as promising.

Since 1929, a limited number of seedlings have been grown as a result of seed produced in pollination work. Three hundred and fifty-eight seedlings, representing crosses of good-quality main-season varieties, are now growing in the experimental orchard. Typical western Maryland apple orchards are shown in figure 8.

Massachusetts

At the Massachusetts Agricultural Experiment Station, Amherst, a number of cross-pollinated seeds resulting from pollination work have been planted from 1925 to date. These include crosses of Red

Astrachan with Cortland, Delicious, and McIntosh; McIntosh with Cortland, Delicious, Northern Spy, and Macoun; Northern Spy with Delicious, McIntosh, and Wealthy; Gravenstein with Wealthy; and Northern Spy selfed.

Minnesota

Apple-breeding work supported by the State of Minnesota was started in 1878, when an annual subsidy administered by the board of regents of the university was granted to Peter Gideon for continuation of his breeding work. Apple breeding organized by and completely under the control of the Minnesota Agricultural Experiment Station was begun about 1890, under the direction of S. B. Green. From 1890 to 1905 several thousand seedlings, largely of Russian varieties, were grown. In 1907 about 4,000 seedlings of Malinda, open pollinated, were planted in the field. About 300 of these have characteristics either of hardiness or fruit quality of sufficient merit to be retained.

From 1907 to 1912 approximately 13,000 seedlings, many from controlled crosses, were grown. In this group of material, 541 trees have been retained for further study. Since 1918, 4,781 seedling trees of hybrid parentage have been grown to fruiting in the breeding plots. The principal crosses are listed in table 3 in the appendix. At the present time, approximately 5,000 trees resulting from crosses made from 1921 to date are being grown to fruiting.

The primary objective in Minnesota is the securing of varieties of good quality that are hardy under the extremely cold winters of that section. Several varieties introduced as a result of the breeding work are listed in table 2, in the appendix.

During the past 100 years a number of individuals have contributed to the list of hardy varieties adapted to this section. The best known of these, Peter Gideon, began planting seed in 1854. He introduced the Wealthy, still one of the leading apple varieties of the United States. Peter, Gideon, and Gideon Sweet were other varieties developed by him. Others in the State who have raised apple seedlings for the specific purpose of developing hardy varieties include G. H. Pond, of Bloomington; John Shaw, of Minnesota City; H. M. Lyman, of Excelsior; Amasa Stewart, of Le Sueur County; Titus Day, of Farmington; Henry Stubbs; and others. A relatively large number of hardy apples have been named as the result of the efforts of these men.

Missouri

Apple-breeding investigations in Missouri are conducted both at the Missouri State Fruit Experiment Station, Mountain Grove, and at the University of Missouri, Columbia. Work at Mountain Grove was started in 1901. In 1935 the six varieties listed in table 2 were introduced.

The primary objective in the early breeding work at the Mountain Grove station was to obtain good storage varieties well adapted to growing conditions in Missouri. With this objective, the principal varieties used included Ben Davis, Winesap, Jonathan, Ingram, and Delicious.

In the breeding work since 1923, the primary objective has been to produce late-blooming varieties with high quality. The principal varieties used include Ralls, Ingram, Mother, Northern Spy, Jona-

than, Delicious, King David, and Golden Delicious. Since 1923, 1,821 seedlings of known parentage have been produced and are now growing in orchard form. Most of these have not yet fruited.

At the University of Missouri, at Columbia, some apple-breeding work has been conducted since 1905. The variety Whitten, from an Ingram × Delicious cross made in 1905 by J. C. Whitten, was introduced in 1925. This is a vigorous tree, a prolific bearer, and has fruit above medium size, yellow blushed with red, and of good quality.

At the present time, 2,732 seedlings resulting from crosses made in 1931 and 1932 at the State Fruit Experiment Station are being grown to fruiting at Columbia. This collection consists mainly of crosses of King David, Wolf River, Ingram, Alexander, Ralls, Twenty Ounce, Rome Beauty, Jonathan, Golden Delicious, Delicious, Mother, Gravenstein, and Northern Spy.

New York

Breeding work with apples at the New York (State) Agricultural Experiment Station, Geneva, was started in 1892, and since that time over 13,000 apple seedlings have been set in the orchard for fruiting, with nearly 2,000 additional now in the nurseries. Over 9,000 of these trees have been set in the orchard since 1922, so the major part of the seedlings have not yet been tested. In producing these 15,000 seedlings, 110 varieties, 10 species, and 63 seedlings have been used as parents. Fifty-five varieties and seedlings have been self-pollinated, but seedlings resulting from these self-pollinations have lacked vigor. Varieties now known to be triploids, including Baldwin, Gravenstein, Rhode Island Greening, and Tompkins King, have given only weak and worthless progeny. Of the diploid varieties, crosses of McIntosh have given by far the greatest number of desirable seedlings. Crosses of Northern Spy and of Yellow Newtown generally produce late-maturing fruit. Yellow Transparent has given early-ripening varieties tart in flavor. Delicious and Deacon Jones have given mostly mild-flavored fruits. Results show that if large-fruited seedlings are desired, large-fruited parents must be used. Sweet flavor appears to behave as recessive, but it is usually impossible to predict just how flavors will be transmitted.

Varieties used most extensively in the breeding work are: Baldwin, 23 times; Cortland, 71; Deacon Jones, 26; Delicious, 38; Early McIntosh, 41; Gravenstein, including Red Gravenstein, 27; Kendall, 26; Macoun, 37; McIntosh, 186; Milton, 31; Northern Spy and Red Spy, 76; Oldenburg, including red sports, 39; Rhode Island Greening, 27; Rome Beauty, including red sports, 57; Wealthy, 32; Yellow Newtown, 30; and Yellow Transparent, 35.

The specific objective of the New York station is to obtain hardy, good-quality apples for dessert and cooking that ripen throughout the season. The most important single need is to secure a high-quality, productive, late-keeping red variety that is fully hardy under New York State conditions. Tree characters desired include early bearing, hardiness to cold winters, self-fruitfulness, sufficiently late blooming to resist spring frosts, and resistance to insects and diseases.

A study of the chromosome constitution of varieties and seedlings is an important part of the breeding program. Crossing of triploid

varieties or of triploid and diploid varieties has produced no new triploid varieties. Chromosome counts on more than 100 resulting seedlings have been made, and all have been aneuploids; that is, having chromosome numbers other than 34 or 51. More than 1,000 such seedlings have been discarded for lack of vigor and fertility. Table 2, in the appendix, lists the varieties introduced as a result of the breeding work at the Geneva station.

There is no formal breeding project at the New York (Cornell) station, Ithaca. At present, about 100 seedling trees of McIntosh crosses, obtained incidentally in pollination experiments, are being grown to fruiting.

Ohio

Apple-breeding work was begun at the Ohio Agricultural Experiment Station, Wooster, by J. B. Keil in 1915. During that year and the year following, crosses were made from which 963 seedlings have fruited. Of these, 25 have been selected for further study or for further use in breeding.

Since 1929, some additional crosses have been made each year by F. S. Howlett and C. W. Ellenwood. From these, 2,414 seedlings are now being grown to fruiting. These later crosses are primarily between Delicious, McIntosh, Gallia Beauty, Northern Spy, Golden Delicious, Cox Orange, Jonathan, Esopus Spitzenburg, Ralls, Rome Beauty, Mother, and some of the numbered selections that resulted from the earlier breeding work. Table 2 in the appendix lists five varieties recently introduced as a result of the breeding work in Ohio.

The specific objectives include (1) to obtain late-blooming varieties that will thus tend to escape the hazards of spring frosts and freezes, and (2) to develop late-keeping varieties whose storage season will extend from February until late spring. A considerable number of seedlings that bloom later than Rome Beauty and Northern Spy, but for the most part derived from these two varieties, have been obtained.

South Dakota

Breeding of apples and other hardy fruits has been a leading horticultural project at the South Dakota Agricultural Experiment Station, Brookings, since 1895. The primary objective is to obtain fruits of fair to good quality that are hardy under the extreme winter cold and frequent summer drought of the northern Plains area. Fully 10,000 apple seedlings of various pedigrees have been grown to fruiting. Much of this has been open-pollinated material. Numerous hybrids between selections of wild crab apples and hardy cultivated apple varieties have been made. As a result of this breeding work, about 25 varieties of crab apples and a considerable number of apples have been introduced. The apples, with their parentage and characteristics, are listed in table 2, in the appendix. Crab apples introduced include Alexis, Amur, Cathay, Beauty, Dolgo, Hopa, Ivan, Izo, Kola, Linda, Maga, Mercer, Missouri Pippin, Nocalyx, Olga, Red Tip, Sapinia, Shoko, Sugar, Tipi, Zapta, Red Flesh, Wakonda, Zelma, Zita, Zaza, Bison, Caputa, Wanblee, Waubay, and Amsib.

Virginia

The apple-breeding program at the Virginia Agricultural Experiment Station, Blacksburg, is not extensive. A number of open-pollinated seedlings have been fruited, of which one from Mother, one from Northern Spy, and three from Delicious appear to have horticultural value. A number of crosses are being made to secure late-blooming, high-quality, and highly colored varieties. Eight hundred fifty-six seedlings of Ralls × Rome Beauty, 622 seedlings of Ralls × Mother, and 1,234 seedlings of York Imperial open-pollinated are now growing in the nursery row.

United States Department of Agriculture

A limited amount of apple breeding has been done by Department of Agriculture workers. From 1912 to 1920, C. P. Close hybridized early varieties with the objective of securing early good-quality varieties in season with Yellow Transparent, or before, and preferably carrying red color. The varieties used included Yellow Transparent, Early Harvest, Early Ripe, Red June, and Red Astrachan. About 400 seedlings representing hybrids of these varieties have fruited in the orchard.

A number of early-ripening selections have been made. Seven of these selections, carrying red color and ripening with Yellow Transparent or earlier, have been distributed for experimental testing. Yellow Transparent has tended to be an excellent parent in the transmission of shape, size, and season of ripening.

Approximately 500 seedling trees of crosses made from 1927 to 1929 are now coming into fruiting at the National Agricultural Research Center, Beltsville, Md. These represent crosses of long-keeping varieties made with the objective of securing good-quality, long storage-season types. The principal parents include Winesap, Yellow Newtown, Granny Smith, Vandervere, and McIntosh.

Promising bud mutations of possible horticultural value originating in various parts of the United States are being grown for comparative testing at Beltsville. The oldest of these selections have now been planted in the orchard 4 years. Additional plantings have been made each year as additional material has been collected. Four trees propagated from each mutation are grown in comparison with parent varieties. In the orchard at the present time are the following bud sports: Baldwin 3, Delicious 30, Gravenstein 5, Jonathan 4, McIntosh 4, Northern Spy 3, Oldenburg 5, Rome Beauty 15, Stark 2, Stayman Winesap 9, St. Lawrence 1, Summer Queen 1, Twenty Ounce 1, Willowtwig 1, and Winesap 20.

Work to develop hardier and better fruits for the northern Great Plains area has been in progress at the United States Northern Great Plains Field Station, near Mandan, N. Dak., since 1915. A large number of Wealthy and other apple and crab apple seedlings have been grown. Several selections from these have been propagated and are being given further test. None has as yet been named. This method of growing quantities of apple seedlings of unknown or partially unknown parentage has been discontinued during recent years, and seedlings of known parentage are being produced at the

present time. About 10,000 apple trees of known parentage are now growing, but only a small part of these have reached bearing age.

A considerable amount of hybridizing between the Siberian crab, *Malus baccata* (L.) Borkh., and standard apple varieties was done in earlier years. These crosses have resulted in seedlings that are hardy and vigorous but have generally small fruits. The varieties being used most largely for hybridizing purposes include Wealthy, Oldenburg, Red Duchess, McIntosh, Delicious, Starking, Yellow Transparent, Haralson, Anoka, and the crab apples Dolgo, Florence, and Whitney.

APPLE BREEDING IN CANADA

Beginning in 1889, a major program was started to develop superior apple varieties sufficiently hardy to withstand rigorous weather conditions in all parts of Canada. At the Central Experimental Farm, Ottawa, seed of Russian varieties planted in 1889 gave 3,000 trees. From this work, only one variety worthy of mention developed—the Rupert, an apple a little earlier than Yellow Transparent and equal to it in quality.

The next step was the crossing of the Siberian crab with named Russian and American apple varieties. Fruits of the first-generation progeny were all under 2 inches in diameter. These, recrossed with apple varieties, gave fruits up to 2½ inches in diameter but lost some of the hardiness of the first-generation hybrids. Most of the fruit of the first-generation hybrids retained the crab characters—long, slender stem; thin, tender skin; and firm, crisp, breaking flesh.

Cross-breeding with better varieties was begun in 1898. Since then, 253 different combinations with 66 different varieties have been made. The variety that has been outstanding as a parent is McIntosh. In one block of 159 trees from open-pollinated McIntosh seed saved in 1898, 27 varieties of sufficient promise for naming were developed. Among these are Melba, Joyce, Macross, Hume, and Lobo. In more recent years, McIntosh has been crossed with the finest quality varieties available. Much of this material has not yet fruited.

In addition to this work carried on at the Central Experimental Farm, breeding is also conducted at the Ontario Agricultural College, Guelph, Ontario, and at the Horticultural Experiment Station, Vineland, Ontario. At Guelph, several thousand seedlings, representing mainly crosses of the McIntosh, Northern Spy, Wealthy, Wagener, and several other varieties, have been fruited. At Vineland, more than 8,000 seedlings have been grown since the work was started in 1915. These represent 130 crosses between varieties, and seed of 65 crosses and selections open-pollinated.

In more recent years the attempts to secure extreme hardiness have been centered at experiment stations in the prairie Provinces, namely, the University of Saskatchewan, Saskatoon, Saskatchewan, and the Dominion Experimental Station at Morden, Manitoba. The most extensive project is at the University of Saskatchewan. Prior to 1930, more than a quarter of a million crosses of apples had been made at that place. The female parents used have been the Siberian crab and the hardiest of the hybrid crab apples such as Osman, Co-

lumbia, Prince, Charles, Tony, and Magnus. The apple varieties have included McIntosh, Melba, Wealthy, Oldenburg, St. Lawrence, and Yellow Transparent.

The largest collection in Canada of the hardiest varieties of apples and crab apples is at the Dominion Experimental Station at Morden. In 1916 some 27,000 open-pollinated seedlings from the hardiest Russian and other varieties of apples were planted. Several thousand of these have fruited, and many are being tested in the prairie Provinces.

A limited amount of breeding work is under way at the Dominion Experimental Station, Summerland, British Columbia. This work consists of crosses of high-quality and long-storage apples. The principal parents used are McIntosh, Yellow Newtown, Winesap, Delicious, Golden Delicious, Rome Beauty, and Grimes Golden. The earliest of these seedlings are just coming into fruiting. Macoun summarized the first 40 years of apple-breeding work in Canada, with the comment that the time should not be far distant when there will be varieties of Canadian apples suitable for all parts of that country where farm development is possible. Experience with breeding apples in Canada indicates the following conclusions, according to Macoun (*13*):

(1) To originate extremely hardy apples:
(a) Cross the apple with the wild Siberian crab and recross the hardiest F_1 with the apple.
(b) Sow seeds of apples that are hardy in other sections having severe climatic conditions.

(2) To originate apples having hardiness, vigor, productiveness of tree, and high quality, good size, and appearance, cross varieties having most of the characteristics desired.

(3) In cross-breeding, where quality is an important factor, cross two varieties that are both good or very good in quality. In crossing a variety of good quality with one of inferior quality, the F_1 will nearly always bear fruit of mediocre quality.

(4) Use parents that have been found by other breeders to transmit their desirable characters to a large degree.

APPLE BREEDING IN EUROPE

The work of European agencies in apple breeding is summarized in the appendix. This summary includes work with the other tree fruits as well as apples, since in most cases several fruits are involved in a single more or less unified breeding program.

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APPENDIX

The following summary includes the more important fruit-breeding stations in Europe.

Czechoslovakia

Průhonice; State Institute for Horticultural Research (director, Ing. Fr. Landovský; chief, Division of Fruit Trees and Nurseries, Ing. J. Souček).—Objective: To secure fruits of better quality with good storage and utilization properties.

Lednice, Morava; Fürst Liechtenstein Plant-Breeding Institute (director, Prof. Dr. Fr. Frimmel).—Extensive breeding investigations of apples and peaches are being conducted. Crosses of several apple varieties are at fruiting age and are being tested in comparison with standard varieties.

England

Long Ashton: Agricultural and Horticultural Research Station, University of Bristol (director, Prof. B. T. P. Barker).—In connection with general fruit investigations, the station conducts breeding investigations on apples, pears, plums, and berries. Several apple varieties, one pear, and four plums have been named and distributed. The objective in the breeding work is to produce high-quality dessert varieties.

East Malling, Kent; Horticultural Research Station (director, R. G. Hatton).—Breeding investigations include the following principal lines:

(1) *Apples*.—Production of rootstocks immune to woolly aphis and conferring disease resistance on the scions; production of fruiting varieties resistant to woolly aphis; production of commercial varieties ripening at times when present English varieties are not available.

(2) *Plums.*—Production of new varieties of rootstock that propagate readily and confer resistance to silver leaf and to bacterial dieback diseases.

(3) *Pears.*—Production of improved varieties of quince stock compatible with pear varieties, and production of commercial pear varieties of high quality.

Merton; John Innes Horticultural Institution (director, Sir Daniel Hall).—The institution is engaged primarily in genetic and cytological research from the standpoint of pure science. When the investigations on inheritance in fruit produce varieties of promise for commercial cultivation, they are selected and given an extended try-out.

(1) *Apples.*—Four thousand seedlings and varieties provide data for the study of the inheritance of characters. About 40 are under extended tests as market varieties. Breeding of rootstocks resistant to woolly aphis, carried on in collaboration with the East Malling station, has yielded seedlings of promise now under trial.

(2) *Plums.*—A large number of seedling plums are being grown in the study of inheritance of characters, particularly of self-incompatibility. Selected seedlings are under trial for commercial value.

(3) *Cherries.*—A large number of varieties of sweet cherry have been raised in the study of cross incompatibility, some of which are now under commercial trial.

Germany

Berlin; Institut für gärtnerischen Pflanzenbau, Friedrich-Wilhelms-Universität (director, Prof. Erich Maurer).—Breeding of tree fruits consists of the selection of vegetatively propagated rootstocks for apples, pears, sweet cherries, and plums. Around 3,000 clons are under observation.

Berlin; Institut für Obstbau, Friedrich-Wilhelms-Universität (director, Prof. Erwin Kemmer).—Investigations on the value of seedlings of varieties and from the wild stocks for stone fruits and pomes.

Geisenheim a.Rh.; Versuchs-und Forschungsanstalt für Wein-, Obst-, und Gartenbau (director, Prof. Dr. Rudloff).—Breeding of tree fruits has been conducted since 1884. A series of new apple and pear varieties has been developed through growing open-pollinated seedlings of named varieties or through hybridization of named varieties. Twelve varieties of pear and seven varieties of apple have been named.

Müncheberg (Mark); Kaiser Wilhelm-Institut für Züchtungsforschung (director, Prof. Dr. Rudorf).—An intensive program of investigation, particularly to develop disease-resistant varieties of fruits. In the apple work, the important objectives are to secure greater resistance to apple scab and to cold and frost, and to develop high-quality market and table varieties. In the work on scab resistance, mass infection of the seedlings of crosses between cultivated varieties and scab-resistant apples is practiced. Over 16,000 apple seedlings are under observation in this work.

(1) *Pears.*—The important objectives are to develop pears resistant to pear scab and to develop high-quality, large-sized summer pears. The testing of resistance to scab is similar to that of apples. Four thousand pear seedlings are under observation.

(2) *Cherries.*—One objective is to secure cherries resistant to brown rot. A large number of crosses of sweet × sour varieties have been tested. Tests of the cross- and self-sterility of the F_1 hybrids of sour × sweet cherries are also being made.

(3) *Plums.*—Testing of strong-growing seedlings of *Prunus cerasifera* from western Asia for their resistance to unfavorable climatic conditions, their adaptation, vigor, productiveness, and fruit quality. These are being crossed with other types of plums. Observations are made of a large number of seedlings of crosses between Mirabelle and Reine Claude types.

(4) *Apricots.*—Seedlings of the vigorous wild apricot of Asia are being tested for their resistance to climatic conditions, adaptation, vigor, productiveness, and fruiting value, and are being crossed with cultivated varieties.

(5) *Peaches.*—A large quantity of seedling material of varieties and crosses between varieties is being tested for the resistance of the buds against late frosts and winter temperatures and the resistance of the trees against peach leaf curl.

Zweigstelle, Naumburg (Saale); Biologische Reichsanstalt für Land- und Forstwirtschaft (director, Dr. Borner).—The objectives are the development of high-quality apple varieties and of stocks that are highly resistant to woolly aphis,

mildew, and scab. A large number of F_1 hybrids between resistant wild types and cultivated varieties are under observation.

Pillnitz a. d. Elbe; Staatliche Versuchs- und Forschungsanstalt für Gartenbau (director, Prof. Schindler).—Investigations on understocks for apples, pears, quinces, plums, cherries, and peaches. The objectives are to obtain good congeniality between stock and scion and to obtain cold resistance and good propagation qualities for the production of clon stocks.

Sweden

Alnarp; Lantbruks-, Mejeri-och Trädgårdsinstitut (director, L. Forsberg).—Investigations are conducted with apples, pears, plums, and cherries. Specially hardy apple varieties producing large yields are crossed with those of fine quality but not hardy in central and northern Sweden. A total of 3,750 seedlings, representing 136 combinations, are being grown. Crosses between triploid and diploid strains have yielded some trees that show promise. Crosses have been made between pear varieties for quality and productiveness, involving 41 combinations and 570 individual trees.

In plum and cherry breeding, difficulty has been experienced in obtaining satisfactory germination. Only one promising type of plum has been secured to date. A small number of crosses between soft-fleshed, high-yielding, early-bearing cherry varieties and the hard-fleshed, sweet varieties have been made.

Union of Soviet Socialist Republics

During the past decade plant explorers from the Soviet Union gathered a central breeding stations in that country much of the available material of the world that may be of promise for production there or for breeding purposes. Under the direction of the Institute of Plant Industry, 14 plant-breeding centers have been set up in different parts of the Union. At these centers, fruit breeding to develop varieties adapted to the different parts of the Union constitutes a major line of investigation. Genetic and cytological studies are being made.

Table 1.—*Origin of important apple varieties*

Variety	Where originated	How originated	When originated
Arkansas (Mammoth Black Twig).	Rheas Mill, Ark.	Chance seedling.	1833.
Arkansas Black	Benton County, Ark	do.	About 1870.
Baldwin	Lowell, Mass	do.	About 1740; widely introduced, 1784.
Ben Davis	Tennessee, Kentucky, or Virginia.		Shortly after 1800.
Black Ben	Washington County, Ark		About 1880.
Bonum	Davidson County, N. C.	Chance seedling.	Cataloged 1860.
Collins	Fayetteville, Ark.	do.	About 1865.
Cortland	New York Agricultural Experiment Station, Geneva.	Ben Davis × McIntosh.	Introduced 1912.
Delicious	Peru, Iowa	Chance seedling	Tree grew about 1880.
Esopus Spitzenburg	Esopus, N. Y.		Probably before 1800.
Fameuse	France or Canada		Distributed by earliest French missionaries before 1700.
Gano	Kentucky or Missouri		About 1875.
Golden Delicious	Porter, W. Va.	Chance seedling	Introduced 1916.
Gravenstein	Europe, probably Germany		Introduced to United States prior to 1826.
Grimes Golden	West Virginia	Chance seedling	Known in 1804.
Haralson	Minnesota Fruit Breeding Station, St. Paul.	Seedling of Malinda	Introduced 1922.
Hubbardston	Hubbardston, Mass	Chance seedling	Known in 1832.
Ingram	Springfield, Mo	Seedling of Ralls	Between 1844 and 1855.
Jonathan	Ulster County, N. Y.	Believed seedling of Esopus.	Described in 1826.
King David	Washington County, Ark.	Chance seedling	Introduced 1901.
Limbertwig	Knox County, Ohio (?)	Seedling	Soon after 1812.
McIntosh	Dundas District, Ontario, Canada.	Chance seedling	Propagated about 1870.
Maiden Blush	First known at Burlington, N. J.		Popular before 1817.
Missouri Pippin	Kingsville, Mo	Chance seedling	Seed planted about 1840.
Northern Spy	East Bloomfield, N. Y.	do.	Planted about 1800.

TABLE 1.—*Origin of important apple varieties*—Continued

Variety	Where originated	How originated	When originated
Northwestern Greening.	Waupaca County, Wis	Chance seedling	Introduced 1872.
Oldenburg (Duchess)	Russia		Imported to United States via England about 1835.
Ortley	New Jersey	Chance seedling	Described in 1817.
Paragon	Fayetteville, Tenn	do	From seed planted about 1830.
Payne	Everton, Mo	do	From seed planted about 1840.
Red Astrachan	Sweden		Imported into United States in 1835.
Red June	North Carolina	Chance seedling	Described as early as 1848.
Rhode Island Greening.	Probably near Newport, R. I.	do	Probably about 1700.
Rome Beauty	Lawrence County, Ohio	do	Introduced 1848.
Roxbury	Probably Roxbury, Mass	do	Prior to 1649.
Smokehouse	Lancaster County, Pa	do	Before 1800.
Stark	Probably Ohio	do	Described 1867.
Starr	Woodbury, N. J.	do	Propagated in 1865.
Stayman Winesap	Leavenworth, Kans	Seedling of Winesap	First fruited in 1875.
Summer Rambo	Europe, probably France	Unknown	Known in United States since 1817.
Tolman Sweet	Probably Dorchester, Mass	Chance seedling	Described in 1822.
Tompkins King (King).	Probably near Washington, N. J.	do	Before 1804.
Twenty Ounce	Unknown; possibly Connecticut.	do	Described in 1844.
Wagener	Penn Yan, N. Y	Seedling	Seed planted in 1791.
Wealthy	Produced by Peter Gideon, Excelsior, Minn.	Seedling of Cherry crab	Described in 1869.
White Pearmain	Unknown; first grown in Indiana.	Unknown	Cataloged in 1858.
Williams	Roxbury, Mass	Chance seedling	About 1750 or before
Willowtwig	Unknown; first grown in Ohio.	Unknown	Described in 1848.
Winesap	Unknown; grown very early in New Jersey.	do	Described 1817; known long before.
Winter Banana	Adamsboro, Ind	Seedling	About 1876.
Wolf River	Wolf River, Wis	do	Introduced 1881.
Yellow Bellflower	Crosswicks, N. J	do	Described in 1817.
Yellow Newtown	Newtown, N. Y	do	Well known as an old tree by 1759.
Yellow Transparent	Russia	Unknown	Imported by U. S. Department of Agriculture, 1870.
York Imperial	York, Pa	Seedling	Propagated about 1830; described 1853.

TABLE 2.—*Apple varieties developed in breeding work at agricultural experiment stations in the United States*

Place of origin and variety	Parentage [1]	Date crossed or seed collected	Date introduced	Characteristics
Iowa Agricultural Experiment Station, Ames:				
Adel	Mixed late	1902	1921	Hardy; Gravenstein type.
Afton	Wolf River × Harrington	1908	1921	Red; midwinter.
Ames	Allen Choice × Perry Russet.	1908	1921	Red; late keeper.
Earlham	Colorado Orange × Allen Choice.	1908	1921	Yellow Newtown type; hardy, late keeper.
Edgewood	Salome × Jonathan	1906	1921	Jonathan type; later keeper; free of Jonathan spot.
Harrington	(?)	1887	1914	Red; midwinter; good.
Hawkeye Greening	Vermont seedling	1900	1921	Large, productive, hardy, culinary fruit.

[1] Parents marked with (?) are somewhat uncertain.

Table 2.—*Apple varieties developed in breeding work at agricultural experiment stations in the United States*—Continued

Place of origin and variety	Parentage	Date crossed or seed collected	Date introduced	Characteristics
Iowa Agricultural Experiment Station, Ames—Continued.				
Joan	Anisim × Jonathan	1906	1932	Large, full red, very productive; November to February.
Macy	Northwestern Greening × Wealthy.	1908	1921	Wealthy type, larger; September.
Maud	McIntosh × Longfield	1906	1922	Red; August-September.
Monona	Wolf River × Harrington	1908	1921	Red, large, perfumed flavor; November-December.
Secor	Salome × Jonathan	1906	1921	Late keeper, best quality.
Sharon	McIntosh × Longfield	1906	1921	Hardy, very good quality; November-March.
Minnesota Agricultural Experiment Station, St. Paul:				
Minnehaha	Malinda, open-pollinated	1907	1920	Hardy, productive.
Folwell	Open-pollinated seedling of Malinda seedling.	1906	1922	Hardy; fruit of good size and quality.
Wedge	Ben Davis, open-pollinated	1908	1922	Vigorous, hardy tree; fruit good size and color; good baking apple.
Haralson	Malinda, open-pollinated	1907	1923	Tree very hardy, productive; fruit attractive; good storage quality.
Beacon	do	1907	1936	Very hardy; fruit early, attractive.
Missouri State Fruit Experiment Station, Mountain Grove:				
Faurot	Ben Davis × Jonathan	1901	1935	Tree resistant to disease; fruit medium size, high color, good storage and dessert quality.
Conard	do	1901	1935	Tree vigorous, disease-resistant; fruit large, colors well; good quality, tart; matures 1 week after Jonathan.
Wright	do	1901	1935	Fruit larger than Jonathan, attractive, colors well; dessert and storage quality good; tree vigorous, productive, very resistant to disease; fruit ripens with Jonathan.
Fyan	do	1901	1935	Tree spreading, vigorous grower, regular producer; fruit large, well colored, attractive; excellent storage quality; fruit ripens 2 weeks after Jonathan.
Grove	Ingram × Delicious	1915	1935	Tree fairly vigorous, spreading, late blossoming, resistant to scab, blotch, and blight; fruit attractive, good size, good quality, colors well; ripening season later than Winesap; excellent keeper.
Whetstone	Conard × Delicious	1915	1935	Tree vigorous, good producer; fruit smooth, large, colors well, uniform in size and shape; excellent storage quality, fair dessert quality.
Missouri Agricultural Experiment Station, Columbia:				
Whitten	Ingram × Delicious	1905	1925	Tree vigorous, prolific; fruit above medium size; yellow with red blush; quality good.
New York Agricultural Experiment Station, Geneva:				
Carlton	Montgomery × Red Astrachan.	1911	1923	Tree vigorous; fruit large, attractive, dark red; flesh white, tender, juicy, sprightly; ripens about with Wealthy.
Cortland	Ben Davis × McIntosh	1898	1915	Tree large, vigorous, spreading, hardy, productive; fruit slightly oblate, large, well colored, quality good; ripens almost with McIntosh but has better storage quality.
Early McIntosh	Yellow Transparent × McIntosh.	1909	1923	Tree vigorous, hardy, productive; fruit red, oblate, attractive; flavor good; season 10 days after Yellow Transparent.

TABLE 2.—*Apple varieties developed in breeding work at agricultural experiment stations in the United States*—Continued

Place of origin and variety	Parentage	Date crossed or seed collected	Date introduced	Characteristics
New York Agricultural Experiment Station, Geneva—Contd.				
Kendall	Zusoff × McIntosh	1912	1932	Tree moderately vigorous, apparently hardy; fruit large, well colored dark red; quality very good; season with McIntosh; possibly better storage quality.
Lodi	Montgomery × Yellow Transparent.	1911	1924	Tree of Yellow Transparent type, vigorous; fruit similar to Yellow Transparent but larger; ripens later.
Macoun	McIntosh × Jersey Black	1909	1923	Tree upright, moderately vigorous; fruit medium size, oblate, dark red, quality very good; season 1 month after McIntosh.
Medina	Deacon Jones × Delicious	1911	1923	Fruit of Delicious type and general quality but more highly colored; slightly later in season.
Milton	Yellow Transparent × McIntosh.	1909	1923	Tree hardy, vigorous; fruit pinkish-red, attractive, crisp, sometimes irregular in shape; quality good; season with Wealthy.
Newfane	Deacon Jones × Delicious.	1911	1928	Fruit of general Delicious type; quality good; in season with Delicious
Ogden	Zusoff × McIntosh	1912	1928	Tree hardy, productive; fruit large, oblate, dark red; quality good; ripens just before McIntosh.
Orleans	Deacon Jones × Delicious	1911	1924	Delicious type; in season with Delicious; keeps longer in common storage.
Red Sauce	Deacon Jones × Wealthy	1910	1926	Large, roundish-conic apple, red, with red flesh to core lines; ripens medium to late.
Sweet Delicious	Deacon Jones × Delicious	1911	1923	Fruits flatter than Delicious; large, sweet, aromatic
Sweet McIntosh	Lawver × McIntosh	1909	1923	Resembles McIntosh in appearance, flavor, and aroma; primarily adapted for home use.
Tioga	Sutton × Northern Spy	1899	1915	Tree large and vigorous, hardy, healthy; fruit large, round-oblate, late, yellow, tart; excellent culinary fruit.
Ohio Agricultural Experiment Station, Wooster:				
Franklin	McIntosh × Delicious	1925	1937	Fruit medium-sized; quality very good; yellow undercolor with bright, attractive red; season with Jonathan.
Downing	Gallia × Kirtland	1929	1937	Fruit above medium to large; very highly colored; quality good; blooming season late; storage to midwinter.
Kirtland	Ingram, open-pollinated	1915	1937	Fruit large, roundish oblate to oblong, attractive, well-colored; quality good; holds in storage till late winter; late blooming.
Warder	Rome, open-pollinated	1915	1937	Fruit medium-sized, roundish oblate, attractive and well colored; storage to end of January; late blooming.
Shaw	Ralls × Mother	1915	1937	Fruit above medium size, roundish oblong; quality good to very good; storage to late winter; late blooming.
South Dakota Agricultural Experiment Station, Brookings:				
Hibkee	Graft hybrid of Hibernal and Milwaukee.		1916	Flesh and core Milwaukee type, surface coloring of Hibernal.
Sereda	Harry Kaump × (Oldenburg?).		1916	Resembles Yellow Transparent in quality and season; yellow; juicy; sprightly.

Table 2.—*Apple varieties developed in breeding work at agricultural experiment stations in the United States*—Continued

Place of origin and variety	Parentage	Date crossed or seed collected	Date introduced	Characteristics
South Dakota Agricultural Experiment Station, Brookings—Continued.				
Caramel	Unknown		1919	Fruit medium size, yellow with red stripes. Fameuse type; sweet; winter apple of high quality. Complete hardiness for far north questionable.
Chance	do		1919	Fruit medium size, oblate, regular, red striped; flesh white; pleasant, subacid; season midwinter.
Sasha	Hibernal × Gravenstein		1919	Fruit medium size, yellow, oblate; sweet, excellent quality; subject to blight.
Chinook	Baldwin × Wild Crab from Minnesota.		1919	Fruit small, oblate, dark red; subacid; season throughout winter; hardy.
Anoka	Mercer × (Oldenburg?)		1920	Fruit medium size, round, striped; flesh white; subacid; season fall; tree very hardy, productive.
Maga	McIntosh × (Virginia Crab?).		1922	Fruit small, flattened, bright-red stripes; quality good; season late.
Goldo	Grimes Golden × (Oldenburg?).		1922	Fruit similar to Grimes Golden in appearance; quality good; tree hardy, vigorous.
Oxbo	Roxbury × (Oldenburg?)		1922	Fruit medium size, juicy, subacid; season late fall.
Bismer	Bismarck × Mercer		1927	Fruit roundish oblate, small, yellow striped with brown-red; flesh yellow; pleasant, subacid to sweet; early bearer; season probably winter.
Elta	Wealthy × (Hibernal?)		1927	Fruit medium to rather small, round-conical; rich orange-yellow, red striped; quality good, sweet; season late fall.
Wakpala	Mercer × Tolman Sweet		1928	Fruit rather small, round, yellow striped with red; flesh white; subacid, spicy, fragrant; late winter.
Tolmo	Tolman Sweet × Oldenburg?).		1932	Fruit medium size, color similar to Oldenburg; flesh white; pleasant, subacid; quality good; season fall.
Volga	Anisim × (Virginia Crab?)		1933	Fruit medium to below, round, conical, bright red; flesh red, fine; juicy, subacid; season late fall.
Lina	Seedling of Malinda		1933	Fruit conical, blushed; mild subacid; culinary fruit.
Kazan	Seedling of Anisim		1934	Fruit round, conical, brilliant red; flesh white; juicy, subacid; flesh red next to skin; fruit rather small.

Table 3.—*Apple crosses of which five trees or more have fruited, and number of promising seedlings resulting, in breeding work at State experiment stations in the United States*

Cross	Locality	Total fruited	Selections retained
		Number	*Number*
Adersleber Calville × Winter Banana	Geneva, N. Y	7	0
Adersleber Calville × Yellow Newtown	do	11	0
Allen Choice × Clemons No. 1	Iowa	41	0
Allen Choice × Perry Russet	do	5	2
Anisim, selfed	do	48	2
Anisim × Gano	do	30	0
Anisim × Jonathan	do	59	1
Anisim × King David	do	12	0
Anisim × Malinda	do	48	3
Anisim × Salome	do	8	0

Table 3.—*Apple crosses of which five trees or more have fruited, and number of promising seedlings resulting, in breeding work at State experiment stations in the United States*—Continued

Cross	Locality	Total fruited	Selections retained
		Number	*Number*
Baldwin × Yellow Transparent	Geneva, N Y	6	0
Barry × Delicious	Iowa	13	0
Ben Davis, selfed	do	5	0
Ben Davis × Allen Choice	do	6	0
Ben Davis × Black Annette	do	41	0
Ben Davis × Delicious	do	44	0
Ben Davis × Esopus Spitzenburg	Idaho	498	8
Ben Davis × Jonathan	do	3 760	34
Do	Mountain Grove, Mo	915	15
Do	Geneva, N Y	12	1
Ben Davis × Longfield	Iowa	20	0
Ben Davis × McIntosh	Geneva, N Y	11	3
Ben Davis × Mother	do	21	2
Ben Davis × Rome Beauty	Idaho	390	2
Ben Davis × Scott Winter	Iowa	6	0
Ben Davis × Wagener	Idaho	1 053	18
Ben Davis × Yellow Newtown	do	57	0
Do	Geneva, N Y	12	4
Black Annette × Salome	Iowa	5	0
Black Annette × Utter	do	35	0
Black Ben × Jonathan	do	5	0
Black Ben × King David	Minnesota	6	0
Black Ben × McIntosh	Iowa	6	0
Black Ben × Oldenburg	Minnesota	48	1
Black Gilliflower × Delicious	Geneva, N Y	6	0
Bloomfield × Delicious	Maryland	19	0
Bloomfield × Oldenburg	do	12	0
Boiken × Charlamoff	Minnesota	12	3
Boiken × Gravenstein	Geneva, N Y	11	0
Boiken × Grimes Golden	do	24	0
Boiken × Macoun	Iowa	7	0
Boiken × McIntosh	do	13	0
Boiken, open pollinated	Minnesota	68	4
Boiken × Wealthy	do	71	1
Briar × Mercer	Iowa	6	0
Brilliant × Black Annette	do	5	0
Brilliant × Malinda	do	31	3
Canada Baldwin × Black Annette	do	5	0
Canada Baldwin × Patten	do	6	0
Canada Baldwin × Winesap	do	22	1
Charlamoff × Black Ben	Minnesota	33	1
Charlamoff × Delicious	do	109	6
Charlamoff × Jonathan	do	9	0
Charlamoff × Stayman Winesap	do	10	0
Chenango × Lodi	Geneva, N Y	8	0
Colorado Orange × Allen Choice	Iowa	25	4
Colorado Orange, open pollinated	Minnesota	56	1
Colorado Orange × Jonathan	Iowa	110	5
Colorado Orange × Oldenburg	Minnesota	20	0
Cortland × Crimson Beauty	Geneva, N Y	22	0
Cortland × Kendall	do	13	0
Cortland × McIntosh	do	20	0
Cortland × Red Spy	do	12	0
Cortland × Yellow Newtown	do	8	0
Cox Orange × Golden Delicious	do	10	0
Cox Orange × Magnet	do	7	0
Cox Orange × Sta 3656 (Lymans Red Fleshed, open pollinated)	do	5	0
Cox Orange × Medina	do	20	0
Cox Orange × Newfane	do	6	0
Daru × Ingram	Missouri	28	2
Deacon Jones × Chenango	Geneva, N Y	15	0
Deacon Jones × Delicious	do	47	9
Deacon Jones × King David	do	8	0
Deacon Jones × Miller Seedless	do	11	0
Deacon Jones × Northern Spy	do	9	0
Deacon Jones × Red Spy	do	20	0
Deacon Jones × Sta 1297 (Deacon Jones × Wealthy)	do	12	0
Deacon Jones × Red Sauce	do	7	0
Deacon Jones × Wealthy	do	41	4
Deacon Jones × Yellow Newtown	do	9	0
Delicious, selfed	Ohio	30	0
Do	Minnesota	6	0

TABLE 3.—*Apple crosses of which five trees or more have fruited, and number of promising seedlings resulting, in breeding work at State experiment stations in the United States*—Continued

Cross	Locality	Total fruited	Selections retained
		Number	*Number*
Delicious × Allen Choice	Iowa	9	0
Delicious × Babbitt	Ohio	7	0
Delicious × Daru	Missouri	28	4
Delicious × Deacon Jones	Geneva, N. Y.	92	2
Delicious × Esopus Spitzenburg	Ohio	11	1
Delicious × Hibernal	Minnesota	36	4
Delicious × Ingram	Missouri	74	1
Delicious × Jonathan	Iowa	7	1
Delicious × Okabena	Minnesota	72	5
Delicious × Oldenburg	do	71	11
Delavan × Clemons No. 1	Iowa	36	0
Dinwiddie × Northern Spy	Ohio	23	1
Dolgo (crab) × Delicious	North Dakota	10	1
Dudley × Scott Winter	Iowa	6	0
Early Harvest × Williams	Maryland	6	0
Early McIntosh × Cox Orange	Geneva, N. Y.	25	1
Early McIntosh × Deacon Jones	do	12	0
Early McIntosh × Primate	do	11	1
Early McIntosh × Red Spy	do	9	0
Early McIntosh × Sta. 845 (Red Canada × Yellow Transparent).	do	5	1
Early McIntosh × Sta. 2391 (Montgomery × Red Astrachan).	do	7	0
Early McIntosh × Sta. 2575 (Montgomery × Yellow Transparent).	do	5	0
Early Ripe × Early Harvest	Maryland	25	0
Early Ripe × Red Astrachan	do	10	0
Early Ripe × Williams	do	17	0
Early Ripe × Yellow Transparent	do	34	0
Esopus Spitzenburg × Ben Davis	Geneva, N. Y.	35	1
Esopus Spitzenburg × Yellow Newtown	Idaho	74	0
Esopus Spitzenburg × Rome Beauty	do	365	5
Esopus Spitzenburg × Wagener	do	279	1
Fameuse × Hubbardston	Ohio	7	0
Gano × Baltimore	Iowa	24	0
Golden Delicious × King David	Geneva, N. Y.	9	0
Golden Delicious × Red Spy	do	9	0
Golden Delicious × Yellow Newtown	do	16	0
Gravenstein × various varieties	do		0
Grimes Golden × Akin	Maryland	22	0
Grimes Golden × Boiken	Geneva, N. Y.	94	0
Grimes Golden × Louise	Ohio	9	0
Grimes Golden × Okabena	Minnesota	34	0
Grimes Golden × Oldenburg	do	459	19
Grimes Golden × Red June	Ohio	9	0
Grimes Golden × Stayman Winesap	Maryland	35	0
Grimes Golden × Wealthy	Minnesota	35	1
Grimes Golden × White Pippin	Ohio	100	3
Grimes Golden × Sta. 7045	Minnesota	16	0
Harrington × Delavan	Iowa	6	0
Harrington × Iowa	do	6	1
Harrington × Ralls No. 18	do	38	3
Helen, open-pollinated	Geneva, N. Y.	5	0
Hibernal × Delicious	Iowa	35	2
Do	Minnesota	20	0
Hyslop × Lady	Geneva, N. Y.	50	0
Ingram, selfed	Mountain Grove, Mo.	7	3
Ingram × Delicious	do	107	11
Ingram × Jonathan	do	Unknown	5
Ingram × Lily of Kent	do	Unknown	1
Ingram × Rome Beauty	Maryland	9	0
Ingram × Salome	Iowa	19	1
Ingram × Twenty Ounce	Mountain Grove, Mo.	Unknown	1
Ingram × Wolf River	do	Unknown	1
Ingram × York Imperial	do	37	1
Iowa × McIntosh	Iowa	21	0
Jersey Black × Canada Baldwin	do	71	0
Jersey Black × Jonathan	do	21	0
Jersey Black × Louise	do	52	0
Jersey Black × McIntosh	do	29	1
Jonathan × Anisim	do	25	0
Jonathan × Delicious	Minnesota	89	17
Jonathan × Esopus Spitzenburg	Idaho	745	3

TABLE 3.—*Apple crosses of which five trees or more have fruited, and number of promising seedlings resulting, in breeding work at State experiment stations in the United States*—Continued

Cross	Locality	Total fruited	Selections retained
		Number	*Number*
Jonathan × Esopus Spitzenburg	Geneva, N. Y	7	0
Jonathan × Hibernal	Minnesota	85	3
Jonathan × Jersey Black	Geneva, N. Y	9	0
Jonathan × Okabena	Minnesota	48	4
Jonathan × Oldenburg	do	477	58
Jonathan × Patten	do	151	10
Jonathan × Rome Beauty	Idaho	193	0
Do	Geneva, N. Y	15	1
Jonathan × Wagener	Idaho	279	0
Jonathan × Wealthy	Minnesota	21	1
Jonathan × Yellow Newtown	Idaho	641	0
King David × Charlamoff	Minnesota	41	5
King David, open-pollinated	do	120	6
King David × Cortland	Geneva, N. Y	9	0
King David × Delicious	Mountain Grove, Mo	6	0
Do	Minnesota	59	7
King David × Grimes Golden	do	8	1
King David × Okabena	do	17	0
King David × Oldenburg	do	279	31
Kinne No. 12, selfed	Iowa	5	0
Kinne No. 12 × Clemons	do	56	0
Lady × Wealthy	Minnesota	81	1
Lawver × McIntosh	Geneva, N. Y	32	1
Longfield × Gano	Iowa	178	2
Longfield × Mountain Beet	do	48	0
Louise × Jersey Black	Geneva, N. Y	20	0
Lymans Red Fleshed	do	15	0
Macoun × Deacon Jones	do	5	0
Macoun × Northern Spy	do	7	0
Maiden Blush × Delicious	Ohio	6	0
Malinda, open pollinated	Minnesota	4,000	300
McIntosh, selfed	Geneva, N. Y	141	0
McIntosh, open-pollinated	Minnesota	132	8
McIntosh × Anis Rose	Geneva, N. Y	10	0
McIntosh × Baldwin	do	30	0
McIntosh × Carlton	do	5	1
McIntosh × Cortland	do	21	0
McIntosh × Cox Orange	do	27	0
McIntosh × Crimson Beauty	do	6	0
McIntosh × Deacon Jones	do	9	0
McIntosh × Delicious	do	56	0
McIntosh × Early McIntosh	do	6	0
McIntosh × Golden Delicious	do	10	0
McIntosh × Jersey Black	do	24	2
McIntosh × King David	do	24	0
McIntosh × Lawver	do	30	0
McIntosh × Lodi	do	36	1
McIntosh × Longfield	Iowa	107	16
McIntosh × Miller Seedless	Geneva, N. Y	36	1
McIntosh × Northern Spy	do	37	0
McIntosh × Rhode Island Greening	do	15	0
McIntosh × Red Spy	do	13	0
McIntosh × Rome Beauty	do	6	0
McIntosh × Sta. 1297 (Deacon Jones × Wealthy)	do	35	0
McIntosh × Sta. 1896 (Delicious × Deacon Jones)	do	39	0
McIntosh × Sta. 1943 (Deacon Jones × Delicious)	do	9	0
McIntosh × Wealthy	do	52	0
McIntosh × Yellow Transparent	do	80	1
McIntosh × Zusoff Winter	do	17	0
Miller Seedless, selfed	do	10	0
Miller Seedless × Deacon Jones	do	5	0
Miller Seedless × Rome Beauty	do	6	0
Miller Seedless, open-pollinated	do	5	0
Milwaukee × Jonathan	Minnesota	48	0
Montgomery × Red Astrachan	Geneva, N. Y	141	5
Montgomery × Yellow Transparent	do	144	0
Mother × Bonum	Maryland	8	0
Mother × Grimes Golden	do	38	0
Mother × Jonathan	Mountain Grove, Mo	Unknown	1
Mother × Ralls	Ohio	5	0
Mountain Beet × Jonathan	Iowa	7	0
Mountain Beet × Ralls No. 18	do	15	0
Mountain Beet × Repka Malenka	do	12	0
Northern Spy × Cortland	Geneva, N. Y	45	0

TABLE 3.—*Apple crosses of which five trees or more have fruited, and number of promising seedlings resulting, in breeding work at State experiment stations in the United States*—Continued

Cross	Locality	Total fruited	Selections retained
		Number	*Number*
Northern Spy × Delicious	Geneva, N. Y.	7	0
Northern Spy × Ingram	Ohio	27	1
Northern Spy × Miller Seedless	Geneva, N. Y.	49	0
Northern Spy × Patten	Iowa	7	2
Northern Spy × Ralls	Ohio	34	1
Northern Spy × Rome Beauty	do	25	1
Northern Spy × Wealthy	Geneva, N. Y.	8	0
Northern Spy × Yellow Newtown	do	65	0
Northwestern Greening × Harrington	Iowa	13	0
Northwestern Greening × Wealthy	do	11	5
Do	Minnesota	23	1
Okabena × Delicious	do	59	1
Okabena × Grimes Golden	do	68	3
Okabena × Oldenburg	do	73	2
Oldenburg, selfed	Iowa	12	0
Oldenburg × Black Ben	Minnesota	42	1
Oldenburg × Colorado Orange	do	17	0
Oldenburg × Delicious	do	376	28
Oldenburg × Gilbert Winesap	do	30	1
Oldenburg × Grimes Golden	do	119	17
Oldenburg × Iowa	Iowa	15	0
Oldenburg × Jonathan	Minnesota	64	1
Oldenburg × King David	do	129	7
Oldenburg × McIntosh	Geneva, N. Y.	1	1
Oldenburg × Stayman Winesap	Minnesota	14	0
Oldenburg × Sta. 7045	do	64	1
Oldenburg × Yellow Transparent	Geneva, N. Y.	12	0
Opalescent × Rome Beauty	do	17	0
Orenco × Cortland	do	12	0
Orenco × McIntosh	do	30	0
Otsego × Miller Seedless	do	69	0
Patten × Colorado Orange	Minnesota	39	1
Patten × Delicious	do	43	1
Patten × Jonathan	do	81	1
Patten × Winesap	do	7	0
Patten × Wolf River	do	144	3
Patten × Sta. 7045	do	74	3
"Patten No. 20" × Jonathan	Iowa	11	2
"Patten No. 20", selfed	do	9	0
"Patten No. 20", open-pollinated	North Dakota	500	3
Pear-shaped Apple, open-pollinated	Geneva, N. Y.	7	0
Perkins, open-pollinated	Minnesota	127	3
Ralls × Alexander	Columbia, Mo.	7	0
Ralls × Delicious	do	8	0
Ralls × Jonathan	do	14	0
Do	Mountain Grove, Mo.	Unknown	3
Ralls × McAfee	do	Unknown	2
Ralls × Mother	Ohio	52	8
Ralls × Northern Spy	do	30	2
Do	Geneva, N. Y.	9	1
Ralls × Romanite	Iowa	7	0
Ralls × Roman Stem	do	522	0
Ralls × Rome Beauty	Ohio	15	0
Do	Geneva, N. Y.	6	1
Ralls × Stayman Winesap	Columbia, Mo.	8	0
Ralls × Wolf River	do	41	0
Rambo × Northern Spy	Ohio	11	0
Red Astrachan, open-pollinated	Maryland	26	0
Red Canada × Boiken	Ohio	12	0
Red Canada × Delicious	do	7	0
Do	Geneva, N. Y.	159	0
Red Canada × Dunwiddie	Ohio	17	0
Red Canada × Yellow Transparent	Geneva, N. Y.	70	1
Red June × Early Ripe	Maryland	9	0
Red June × Yellow Transparent	do	10	0
Red Spy × Cortland	Geneva, N. Y.	5	2
Red Spy × Cox Orange	do	47	2
Red Spy × Delicious	do	40	0
Repka Malenka × Black Annette	Iowa	104	5
Rhode Island Greening × Cortland	Geneva, N. Y.	5	0
Roman Stem, selfed	Iowa	7	0
Roman Stem × Grimes Golden	do	35	0
Roman Stem × Jonathan	do	101	1
Roman Stem × Wealthy	do	5	1

Table 3.—*Apple crosses of which five trees or more have fruited, and number of promising seedlings resulting, in breeding work at State experiment stations in the United States*—Continued

Cross	Locality	Total fruited	Selections retained
		Number	*Number*
Rome Beauty × Esopus Spitzenburg	Geneva, N Y	10	0
Rome Beauty × Jersey Black	do	16	0
Rome Beauty × Jonathan	do	20	0
Rome Beauty × McIntosh	do	70	0
Rome Beauty × Northern Spy	Ohio	6	0
Do	Geneva N Y	9	0
Rome Beauty × Oldenburg	Minnesota	31	2
Rome Beauty × Opalescent	Geneva, N Y	[illegible]	1
Rome Beauty × Yellow Newtown	Idaho	843	0
Rome Beauty × Wealthy	Geneva, N Y	5	0
San Jacinto × Esopus Spitzenburg	Ohio	32	0
San Jacinto × Starr	Geneva, N Y	9	0
San Jacinto × Williams	do	45	1
San Jacinto × Yellow Transparent	do	43	0
Scott Winter × Salome	Iowa	17	0
Silken Leaf × Delicious	do	13	0
Stayman Winesap × Black Ben	do	5	0
Stayman Winesap × Grimes Golden	Maryland	14	0
Sutton × Northern Spy	Geneva, N Y	7	2
Tolman Sweet × Ben Davis	Iowa	11	0
Wagener × Grimes Golden	Idaho	144	0
Wagener × McIntosh	do	1	0
Wagener × Rome Beauty	do	1 144	7
Washington Black Beauty open pollinated	Minnesota	40	4
Wealthy, selfed	Ohio	397	6
Wealthy × Allen Choice	Iowa	33	0
Wealthy × Baltimore	do	10	2
Wealthy × Ben Davis	do	104	3
Wealthy × Clemons	do	9	0
Wealthy × Colorado Orange	do	[illegible]	1
Wealthy × Delicious	Minnesota	17	1
Wealthy × Gano	Iowa	[illegible]	0
Wealthy × Jonathan	do	21	2
Wealthy × Lady	Minnesota	21	1
Wealthy × Okabena	do	88	10
Wealthy × Oldenburg	do	17	0
Wealthy × Roman Stem	Iowa	18	1
Wealthy × Wolf River	Minnesota	109	3
Wealthy × Sta 7045	do	45	1
White Pippin × Grimes Golden	Ohio	21	1
Williams × Yellow Transparent	Maryland	14	0
Winesap × Anisim	Iowa	9	0
Winesap × Grimes Golden	Ohio	16	0
Winesap × Jonathan	Iowa	23	0
Winesap × Willowtwig	do	12	0
Wolf River × Allen Choice	do	6	0
Wolf River × Harrington	do	5	3
Wolf River × Yellow Transparent	Maryland	19	0

Table 4—*Locations and personnel of apple-breeding work in the United States*

State, institution, and location	Date begun	Previous workers	Present staff
Idaho			
Agricultural Experiment Station, Moscow	1909	C C Vincent 1909-33	Lief Verner
Illinois			
Agricultural Experiment Station, Urbana	1908	C S Crandall, 1908 29	J C Blair, M J Dorsey, J S Whitmire
Iowa			
Agricultural Experiment Station, Ames	1880	J L Budd 1880-1905 S A Beach, 1905-22	H L Lantz, T J Maney, B S Pickett
Maine			
Agricultural Experiment Station, Orono	1911		R M Bailey
Maryland			
Agricultural Experiment Station, College Park	1906	C P Close, 1906-11, W R Ballard, 1912-18 E C Auchter, 1919-28, W E Whitehouse, 1921-29	A L Schrader, S W Wentworth

Table 4.—*Locations and personnel of apple-breeding work in the United States*—Con.

State, institution, and location	Date begun	Previous workers	Present staff
Massachusetts:			
Agricultural Experiment Station, Amherst.	1925		J. K. Shaw.
Minnesota:			
Agricultural Experiment Station, St. Paul.	1890	S. B. Green, Charles Haralson, M. J. Dorsey, J. H. Beaumont.	W. H. Alderman, A. N. Wilcox, W. G. Brierley, E. Angelo, F. E. Haralson.
Missouri:			
State Fruit Experiment Station, Mountain Grove.	1901	John T. Stinwon, Paul Evans, F. W. Faurot.	Paul H. Shepard.
Agricultural Experiment Station, Columbia.	1905	J. C. Whitten, W. H. Chandler.	A. E. Murneek.
New York:			
Agricultural Experiment Station, Geneva.	1892	S. A. Beach, 1891–1905	U. P. Hedrick, Richard Wellington, G. H. Howe, B. R. Nebel.
Ohio:			
Agricultural Experiment Station, Wooster.	1915	J. B. Keil	F. S. Howlett, C. W. Ellenwood.
South Dakota:			
Agricultural Experiment Station, Brookings.	1895		N. E. Hansen.
Virginia:			
Agricultural Experiment Station, Blacksburg.	1910	A. W. Drinkard, Jr.	Fred W. HofMann.
U. S. Department of Agriculture, Bureau of Plant Industry:			
Arlington, Va.; Beltsville, Md.	1912	C. P. Close	H. P. Gould, J. R. Magness.
Mandan, N. Dak.	1915	Max Pfaender	W. P. Baird.

PROGRESS IN PEAR IMPROVEMENT[1]

J. R. MAGNESS, Principal Pomologist,
Division of Fruit and Vegetable Crops
and Diseases, Bureau of Plant Industry

THE pear, like the apple, first came to us from western Asia by way of European countries. Its history in Europe closely parallels that of the apple. Apparently indigenous in the region from the Caspian Sea westward into Europe, whence so many of our fruits came, the pear was doubtless used as food long before agriculture was developed as an industry. Hedrick, in the Pears of New York, gives an excellent summary of its history and development during the last 3,000 years.

Nearly 1,000 years before the Christian Era, Homer listed pears as one of the fruits in the garden of Alcinous, thus indicating that they were known to the Greeks of his day. Prior to the Christian Era at least a few varieties were known. Theophrastus (370–286 B. C.) mentioned both wild pears and cultivated named varieties and described grafting. Pliny, of ancient Rome, named more than 40 varieties. With the migrations of the Romans the pear was distributed throughout temperate Europe.

At the time of the discovery of North America, a number of varieties were known in Italy, France, Germany, and England, but there was little progress in the culture of the pear, at least as far as is known, from the early Christian Era until about the beginning of the sixteenth century.

During the eighteenth and nineteenth centuries, there was a tremendous interest in pear breeding and improvement, particularly in Belgium and France. Hardenpont (1705–74), a priest in Mons, Belgium, sowed large quantities of pear seeds and introduced a dozen varieties having soft, melting, buttery flesh. Prior to his time only types with crisp, breaking flesh were known. Whether or not he did any hybridizing is not known. Van Mons (1765–1842), a physician and pharmacist at Louvain, Belgium, developed pear breeding on a large scale. At one time 80,000 seedlings were growing in his gardens. He originated or distributed over 400 varieties, 40 of which have proved of lasting merit.

Many other Belgian and French pear breeders were working on a smaller scale and introduced varieties of great value. The nineteenth century may well be considered the golden era of pear breeding in these countries. Most of the breeding consisted in planting seed of open-pollinated varieties and in selecting the superior types.

[1] This report is made possible only through the cooperation of staff members of the State agricultural experiment stations conducting pear-breeding investigations. Reports for their respective stations were submitted by W. H. Chandler and W. P. Tufts, of California; H. P. Stuckey, of Georgia; A. L. Schrader, of Maryland; A. N. Wilcox, of Minnesota; G. H. Howe, of New York; and F. C. Reimer, of Oregon.

The pear in Europe today, derived from *Pyrus communis* L., takes its place beside the apple in total production, in diversity of varieties, and in popularity. It is far more popular in Europe than in the United States.

THE PEAR IN NORTH AMERICA

THE early history of pear growing in North America parallels that of apple growing. Pear seed was brought to this country by the early settlers and possibly trees of some varieties. Pear trees were a part of the early colonial orchards. The Prince Nursery catalog listed 42 varieties in 1771.

About that time, however, fire blight or pear blight, the scourge that has frustrated the development of the pear industry in the United States ever since, became epidemic. William Denning, describing the disease in 1794, says he first saw it in 1780 in orchards of the Hudson Valley. How much earlier it might have occurred we do not know, neither are we sure where it came from. It seems most probable that it was present in some native host and became epidemic only when considerable orchard development occurred. Not for another century was the cause of the disease known. In 1882, Burrill, at the University of Illinois, discovered the cause of fire blight to be a bacterium working in the bark tissues.

The disease, which attacks roots, crown, trunk, limbs, blossoms, fruit, and leaves, proved such a menace that pear growing with varieties from Europe, or with seedlings produced from them, never developed to a major industry in the eastern United States. Only in a few sections having relatively cool summers and mild winters has the culture of the European type of pear been successful in the Eastern States. Such conditions are found in relatively narrow strips on the south and east sides of Lake Michigan, Lake Erie, and Lake Ontario. Elsewhere the warm, humid summers have been so

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ALL *of the known species of pears are native to Europe, Asia, and northern Africa. There are no native American species, and none are known in the Southern Hemisphere. Within these species and varieties, however, we have all the characters needed to produce pears suitable for this continent—fruit of high quality, winter-hardy, and above all resistant to fire blight, the scourge that has made the growing of superior pears impossible throughout much of the United States and difficult even in favored regions. To combine these characters properly constitutes a great challenge to the American plant breeder. He has made a small but promising start, and if, with the raw materials available, the problem is not solved within the next century, it will indeed be a reflection on his scientific ability and energy.*

favorable for fire blight that the development of commercial orchards with these types of pears has not been very successful (fig. 1).

An event of great importance from the standpoint of eastern pear growing was the introduction of the Chinese or sand pear into the United States. The sand pear (*Pyrus serotina* Rehd.) was growing in the United States by 1840, apparently having come in by way of Europe. These pears are relatively resistant to blight. They are coarse-fleshed, generally contain many grit cells, and are themselves of very inferior quality. Because of their blight resistance, however, they were rather widely disseminated over the eastern United States.

Figure 1.—Pear orchard destroyed by fire blight.

Soon hybrids between the sand pear and *P. communis* varieties began to appear. The Le Conte, Kieffer, Garber, Douglas, and more recently the Pineapple, are the most important of these hybrids. All of these are very inferior in quality as compared to the "buttery" pears of Europe. They are sufficiently resistant to blight, however, to permit growing in most parts of the eastern United States. They are widely planted in home orchards and in small commercial orchards at the present time.

Another event of importance was the importation of a large number of varieties from northern Russia. Since 1879, when the first shipment was made, 70 to 80 varieties have been brought in and tested in Iowa and other northern sections. These are hardy but generally poor in quality and very subject to blight. They are of value only for breeding for hardiness, and probably some of the oriental types that combine hardiness and blight resistance are superior for this purpose.

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In the United States the greatest development of pear growing has centered in the moderately warm, dry valleys of the three Pacific Coast States. Pears were established in California long before that State became a part of the Union, having been introduced by the Mission Fathers with the earliest white settlements. In the valleys of the Pacific States, where there is little summer rainfall and the nights are relatively cool, fire blight is less rampant than in the eastern United States. Most of the European varieties reach a high degree of perfection in these areas. Although blight is a constant menace in many of the sections at the present time, methods have been developed so that it is possible to control it commercially, chiefly by means of careful surgery.

The principal pear varieties grown in the United States today are listed in the appendix, with notes on their origin.

It is apparent that, in contrast to apples, our highest quality pear varieties have mainly been imported directly from Europe. The most important—Bartlett, Anjou, Bosc, and Winter Nelis—are all direct European importations. Among our leading varieties, only those selected primarily because of blight resistance have originated in the United States. These include Seckel, a blight-resistant variety apparently of straight *Pyrus communis* origin, and the *P. communis* × *P. serotina* hybrids. European breeders have worked with pears to a far greater extent than with apples, and in all respects except resistance to fire blight their best varieties have so far proved superior to those that have developed as chance seedlings in the United States.

Objectives in Pear Breeding in the United States

One objective stands out above all others in the breeding of pears in the United States. This is to secure resistance to fire blight, combined with satisfactory dessert quality. In few regions east of the Rocky Mountains can varieties be grown successfully unless they have a fairly high degree of blight resistance. Varieties available at the present time that have fair blight resistance—primarily *Pyrus communis* × *P. serotina* hybrids—are all of inferior quality as compared to the better *P. communis* varieties. The securing of blight resistance coupled with quality is important in every section of the United States and is the predominent need in at least three-fourths of the potential pear-growing territory of the country.

A second and more localized objective is the securing of additional hardiness in pear varieties for growing in the northern Great Plains and other areas that have very cold winters. Varieties of *Pyrus communis* having good dessert quality do not possess sufficient hardiness to thrive in those regions.

Blight-resistant varieties are needed that also have high dessert and culinary quality and that ripen at intervals from early summer until late fall. Late-ripening varieties with good storage quality are especially needed. At the present time no varieties are available that have these characteristics and are adapted for growing east of the Rocky Mountains. Varieties of European origin meeting these qualifications are grown successfully in the Western States, but even there the problem of blight control is of tremendous importance and involves a heavy expense to growers.

Rootstocks are also needed that combine blight resistance with satisfactory hardiness, congeniality to scions, and adaptation to environment. Fire blight frequently attacks the roots as well as the tops of the trees, and rootstocks that are blight-resistant are a primary need in most regions of the United States where pear growing is attempted.

Material Available for Pear Breeding in the United States

The cultivated pear varieties of Europe, derived from *Pyrus communis*, generally produce fruit of high quality. Superior varieties produced by European breeders have the buttery texture, relative freedom from grit cells, and aromatic to spicy flavors needed in pears of high quality. While these varieties vary considerably in blight resistance, none of the high-quality European sorts are known to be sufficiently resistant to thrive in the regions where blight is most serious.

The snow pear, *Pyrus nivalis* Jacq., native to southern Europe and cultivated there for making perry, the fermented pear juice popular as a beverage in Europe, is not cultivated in the United States. Trees of this species are very susceptible to blight, and it appears to have little merit as breeding material except possibly for developing perry types if a perry industry should be built up in this country.

The sand pear, *Pyrus serotina*, is native to central and eastern China and is cultivated in China and Japan. The fruit is heavily russeted and commonly apple-shaped, and the flesh is very gritty. Trees of this species are variable in resistance to fire blight but on the average much more resistant than *P. communis*. It hybridizes freely with *P. communis* varieties, and several of the hybrids are important American varieties because of their blight resistance, although all are lacking in quality.

The Ussurian pear, *Pyrus ussuriensis* Maxim., is native to northern China and eastern Siberia. This is the hardiest of pears. The tree is a rather slow grower but very resistant to blight. It is cultivated, and a number of varieties are known in its native habitat. The best of these varieties are soft-fleshed, not excessively gritty, juicy, and subacid to acid in flavor. The trees bloom very early. This appears to be an extremely valuable species for breeding to obtain blight resistance and hardiness.

The Callery pear, *Pyrus calleryana* Decne., is native to central China. The trees are medium to large, vigorous, and bloom early. The fruit is small and seems valueless. The trees are very blight-resistant and may be valuable as stocks for regions having mild winters. They are of questionable hardiness for the colder sections.

The birchleaf pear, *Pyrus betulaefolia* Bunge, is native to central and northern China. The tree is large and vigorous. It blossoms late and produces small, valueless fruit. Many trees of this species are quite susceptible to blight, but there are some resistant types. This species propagates readily from root cuttings, so the blight-resistant types are of possible value for rootstock purposes.

Although there are several other species—a total of 20 to 25 according to the usual botanical classifications—the 6 listed above seem to be of greatest economic importance. All of these species will, so far as known, hybridize readily among themselves.

It is of interest to note that all of the known species of pears are native in Europe, Asia, and northern Africa. There are no native American species; neither are any known in the Southern Hemisphere. Within these species and their varieties we have all of the characters—high-quality fruit, blight resistance, and hardiness—needed to produce pear varieties suitable for North American conditions. To combine these characters in varieties adapted to the different regions of the United States constitutes a great challenge to the American plant breeder. Only a small start has been made on this problem. With the raw materials available, however, if American plant breeders do not solve this problem within the next century it will indeed be a reflection on their scientific ability and energy.

Figure 2.—Blossoming spurs of pear, in proper stage of development for emasculation

Pear-Breeding Work Now in Progress in the United States

The technique of collecting pollen, emasculating blossoms (fig. 2), and cross-pollinating in pears is in all respects similar to that already outlined for apples.

Pear breeding at the California Agricultural Experiment Station was started in 1928. The objective is to obtain superior *Pyrus communis* varieties ripening at intervals throughout the season, including some with good storage quality for holding through the winter months. Approximately 1,700 open-pollinated seedlings of the leading *P. communis* varieties are being grown. In 1931, crosses to give approximately 3,000 seedlings were made. These consisted of Bartlett crossed with Winter Nelis, Easter Beurré, Comice, Hardy, Anjou, P. Barry, and Bosc.

At the Georgia Experiment Station at Experiment, Ga., a considerable collection of varieties is maintained and studied for resistance to blight. Active breeding work is not under way. The variety Sowega, introduced in 1930 by J. J. Parish, Adel, Ga., is reported to be of high quality and very resistant to blight.

Pear-breeding work in Iowa was started by C. G. Patten shortly after 1867. The assistance Patten received from public institutions has been outlined briefly in connection with his work with apples. Patten's work was significant in demonstrating the possibility of developing pears sufficiently hardy to thrive in the upper Mississippi Valley. He grew a large number of open-pollinated seedlings of *Pyrus ussuriensis*. This oriental pear was growing adjacent to *P. communis* varieties, and many of the seedlings are obviously hybrids. The

seedling trees were more vigorous than the original *P. ussuriensis* and proved as "hardy as an oak." These hybrids have proved more hardy in tests during the last 20 years than pears from any other source. Twenty-five of Patten's seedling pears have been selected for further breeding work. One variety, the Patten, a cross of Orel 15 × Anjou, was introduced by the Iowa Agricultural Experiment Station in 1922. Crosses and backcrosses of Patten's seedlings with *P. communis* varieties were made between 1918 and 1928. Much of this work was lost when it was necessary to abandon the station in 1932.

Pear-breeding work at the University of Maryland, College Park, was begun in 1905. Hybrids consisted mainly of crosses of Kieffer with *Pyrus communis* varieties, particularly Seckel and Anjou, although a few crosses of *P. communis* × *P. communis* were made. A total of 1,411 seedlings from crosses made between 1905 and 1917 have been grown to fruiting. Only one, a Kieffer-Anjou hybrid, seems to have merit. A number of these hybrids are being maintained for further determination of their blight resistance.

In Michigan during the period between 1916 and 1919, W. F. Wight and Don Ward, of the United States Department of Agriculture, hybridized pears at the South Haven Horticultural Experiment Station at South Haven. These hybrids were grown to fruiting cooperatively by the Department and the South Haven station. The parents were for the most part moderately blight-resistant types of good quality. Of all the crosses made, Barseck × Bartlett has been most outstanding. A number of the progeny of this cross have produced pears of excellent quality, apparently with some blight resistance, the degree of which has not been satisfactorily determined. A number of these selections are under test in Michigan and at the United States Horticultural Station at Beltsville, Md.

A limited amount of breeding work was started at the Minnesota Agricultural Experiment Station in 1908. The primary objective has been to obtain hardiness and blight resistance. In that year, 300 seedlings of an unknown variety from Manchuria were planted. Two of these have been selected as of horticultural value. Since 1924, a considerable number of hybrids of *Pyrus communis* × *P. ussuriensis* have been made. These are grown in the field without any protection, and only the hardiest survive for planting in the trial orchards. Approximately 700 of these seedlings have survived the Minnesota winters and are being grown to fruiting.

Pear breeding at the New York (State) Agricultural Experiment Station at Geneva started in 1892. Relatively few seedlings were grown before 1906. By 1921, 1,775 seedlings had been grown, most of which have fruited. Approximately 5,000 seedlings have been set out since 1921, of which only a few have fruited as yet. The varieties used in crossing and the number of times they were used are as follows: Anjou, 31; Bosc, 59; Bartlett, 85; P. Barry, 11; Clairgeau, 16; Cayuga, 16; Dana Hovey, 12; Ewart, 10; Gorham, 13; Kieffer, 24; Lincoln Coreless, 12; Ovid, 9; Phelps, 35; Pulteney, 41; Seckel, 77; Sheldon, 20; Tyson, 28; Winter Nelis, 17; and Willard, 17. The New York work has consisted primarily in the hybridizing of *Pyrus communis* varieties to produce high-quality types. The objective has been to obtain pears equal to Bartlett in size, appearance, and quality, but ripening through

a long season. Recently, added emphasis has been placed on the testing of all seedlings for blight resistance. The varieties introduced as a result of the breeding work in New York State are listed in the appendix.

By far the most extensive project in the United States on the testing of known varieties and species of pears for their resistance to blight has been conducted at the Southern Oregon Branch Experiment Station, Talent, Oreg. (fig. 3). Tests have included practically all of the known species, as well as a number of the Asiatic varieties of *Pyrus serotina* and *P. ussuriensis*. Eighty-five *P. communis* varieties and hybrids have been inoculated repeatedly, while 500 pear varieties have been grown in orchard form where they were exposed to natural infection from great quantities of blight in the orchard. The earlier results of these experiments are recorded by Reimer (*7*).[2] This work gives much information on the relative blight resistance of various *Pyrus* species and varieties and indicates clearly the material of greatest value for breeding for blight resistance.

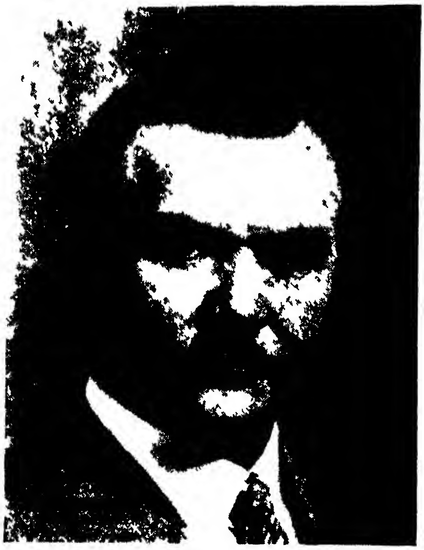

Figure 3.—F. C. Reimer, whose extensive work in determining the extent of blight resistance in practically all known species and varieties of pears serves as a foundation in breeding for blight resistance.

The present work has two objectives—(1) to develop dependable, hardy, congenial, blight-resistant rootstocks for pears; and (2) to develop high-quality, blight-resistant varieties. Ba Li Hsiang, a highly resistant *Pyrus ussuriensis* variety, pollinated with another resistant variety, gave seedlings sufficiently blight-resistant for rootstocks, but such seedlings have proved unsatisfactory for some of the commercial *P. communis* varieties and have been discarded. Seedlings of *P. calleryana* resulting from resistant trees planted so that both pollen and seed parents are resistant have proved highly resistant to blight and appear to be excellent rootstocks in southern Oregon. They may lack sufficient hardiness for the colder sections of the country. By mass selection methods, seedlings of *P. communis* have been found resistant to blight. From 10,000 seedlings, 10 proved highly resistant, and these 10, when pollinated with other resistant varieties, transmit a high degree of resistance. Three of these have produced seedlings 100-percent resistant to root blight when pollinated with another resistant type.

In breeding for resistant varieties of high quality, varieties of *Pyrus ussuriensis* crossed with Anjou, Bartlett, Bosc, and Comice have given only poor-quality varieties, and all have been discarded, though a part of the seedlings were blight-resistant.

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[2] Italic numbers in parentheses refer to Selected References to Literature, p. 627.

In 1915, Reimer saw a small Anjou seedling on Benjamin Buckman's farm at Farmingdale, Ill., which was just coming into bearing, with fruit of good size and mediocre quality. The tree was free from blight while the disease was rampant in other varieties surrounding it. Scion wood was obtained and the tree propagated at the Southern Oregon Experiment Station. Extensive inoculation work at the station has proved that this tree is highly resistant to blight. Buckman named the tree Farmingdale in honor of his town.

During the last 5 years several thousand trees have been produced which are crosses between Farmingdale and Anjou, Bartlett, Bosc, Comice, and Seckel. Approximately 75 percent of these seedlings have blighted when inoculated. The remainder have so far proved highly resistant even when repeatedly inoculated. The oldest of these crosses should come into bearing during the next year or two. It is hoped that among these resistant trees at least a small number will possess the good quality of the fine-flavored varieties used as one parent in each cross and the blight resistance of the Farmingdale.

Figure 4.—Merton B. Waite, whose experiments in the United States Department of Agriculture showing the necessity for cross-pollination in horticultural varieties of pears led the way to the great amount of research conducted since, not alone with pears but with all orchard fruits. He was also an early leader in breeding pears for blight resistance.

With one exception, all the crosses have proved vigorous. This one exception is Anjou × Farmingdale, these seedlings being only moderately vigorous. Furthermore, the leaves of 20 percent of the seedlings resulting from this cross possessed a waxy white color (devoid of chlorophyll), and the seedlings died when they were from 2 to 4 inches high. This is probably the result of inbreeding, since Farmingdale itself is a seedling of Anjou.

Breeding work to obtain pear varieties resistant to blight was started at the Tennessee Agricultural Experiment Station in 1925, though a limited amount of hybridizing had been carried on earlier. The work since 1925 has consisted of crossing resistant species such as *Pyrus serotina*, *P. ussuriensis*, and *P. calleryana* with the more resistant varieties of *P. communis*. Approximately 3,000 seedlings from these crosses are now being grown, and additional hybridization is under way.

In the United States Department of Agriculture breeding investigations to develop pear varieties resistant to fire blight were started

by M. B. Waite at the Arlington Experiment Farm, Arlington, Va., about 1908 (fig. 4). The early work consisted of crossing Kieffer with Seckel, Anjou, and Bartlett. Several thousand seedlings from these crosses have been grown to fruiting. Several selections made from these earlier seedlings combine good fruit quality with blight resistance. At least one selection seems to be very blight-resistant and has good fruit characters from the standpoint of flesh texture,

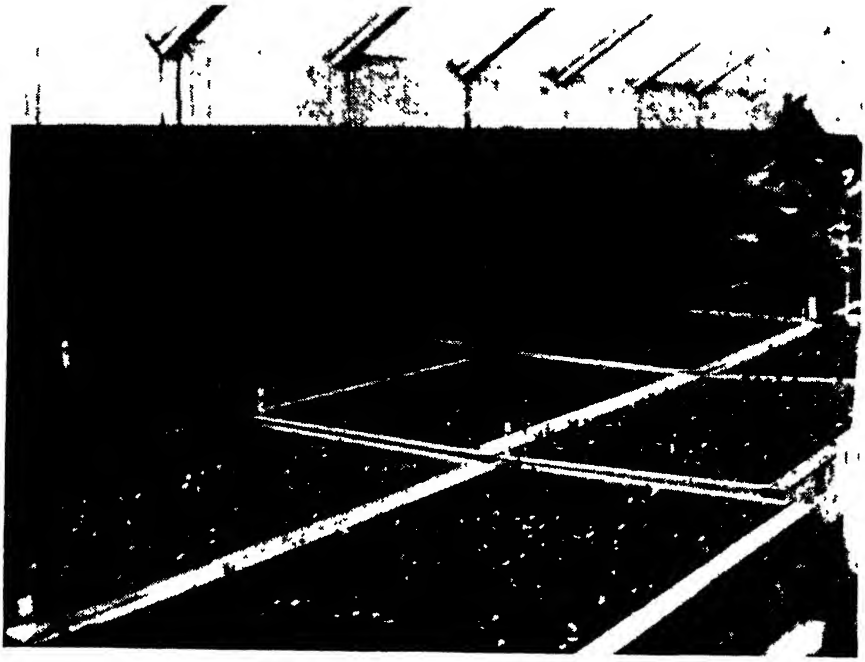

Figure 5.—Hybrid pear seedlings growing in the greenhouse.

size, and quality. None of the selections has been named, but they are worthy of general testing. At the present time, around 5,000 seedlings from the above crosses are being grown to fruiting (fig. 5). These are inoculated with blight each year in addition to being exposed to field infection. Resistance to blight, resistance to leaf spot, and fruit characters are being recorded.

A few crosses between high-quality *Pyrus communis* varieties have been made at Palo Alto, Calif., by W. F. Wight, of the United States Department of Agriculture. The purpose in these crosses is to obtain pears of high dessert quality, ripening at intervals through the summer, and also varieties suitable for winter storage.

A list of pear material of special value for breeding purposes, with the institutions at which it is maintained, is given in the appendix. Some of the results of hybridization are illustrated in figure 6.

For a discussion of pear-breeding work under way in other countries, see pages 602–604.

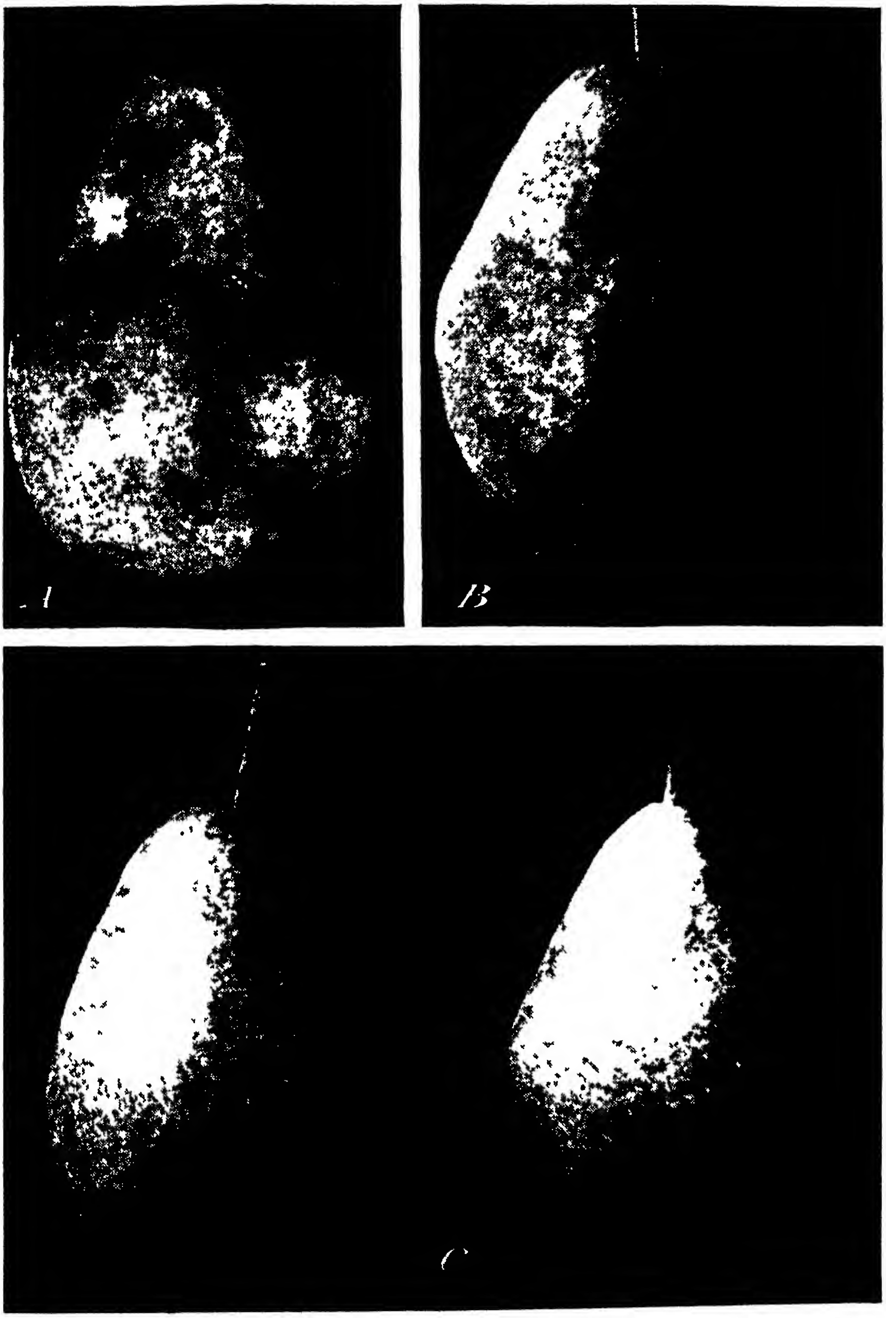

Figure 6.—The fruits of hybridization: *A*, Bartlett pear (*Pyrus communis*); *B*, Kieffer a hybrid of *P. serotina* × *P. communis*; *C*, hybrid variety from a cross of Kieffer × Bartlett.

CYTOLOGY AND GENETICS OF THE PEAR[3]

THE basic chromosome number in the germ cells of pear species is 17, the same as that of the apple. Among European varieties, approximately one-fourth to one-third of those examined to date are triploids, this ratio being about the same as for apples in the United States. These forms with 51 somatic chromosomes, like the triploid apples, generally produce only a small percentage of viable pollen. According to unpublished data from the New York (State) Agricultural Experiment Station, all of the pear varieties important in the United States are diploids with 34 chromosomes in the vegetative tissues. Most of these diploid varieties produce a relatively high percentage of viable pollen.

Recently two bud mutations that may be tetraploids have been found in pears, one in Bartlett, the other in Winter Nelis. These produce giant fruit similar in general appearance to the parent variety but coarser textured. In the case of the Bartlett at least, the fruit is inferior in quality to the parent variety. If cytological examination proves these to be true tetraploids, they may prove to be of much interest and value from the standpoint of breeding, as crosses of tetraploids with diploid varieties should produce triploids.

Few studies have been reported to indicate the type of inheritance that may be expected in pears. Since all varieties of *Pyrus communis* are highly heterogeneous, and since selfing in most varieties is impracticable because of failure of self-pollinated blossoms to produce viable seed, inheritance studies are difficult.

Size of fruit appears to be controlled by many factors. Seckel gives mainly small-sized fruits even when hybridized with large-fruited types, though many intermediate-sized fruits are found in the progeny, a few approaching the size of the larger parent.

The low quality of oriental pears seems to be dominant over high quality of other groups, though intermediate forms sometimes are found. No high-quality progeny has occurred in F_1 hybrids of *Pyrus serotina* × *P. communis* or *P. ussuriensis* × *P. communis*. In backcrosses of these F_1 hybrids with high-quality *P. communis* varieties, some good-quality types result. In 11 trees from Kieffer (*P. communis* × *P. serotina*) × Anjou, fruited in 1936 by the Bureau of Plant Industry, fruits of 2 rated good and 4 fair to good. In 132 Kieffer × Seckel hybrids, fruit of 17 rated as good and 24 as fair to good in quality.

Kieffer, a sand pear hybrid, probably carries russet as a recessive character. In the crosses with russeted Seckel, 23 hybrids were heavily russeted, 45 semirusseted, and 64 smooth. These results indicate that in this cross russet is recessive to smooth skin. Kikuchi has reported that within *Pyrus serotina*, russet behaves as a dominant. In 122 Kieffer (subacid) × Seckel (sweet) hybrids, 26 produced sweet fruit, like Seckel, 82 subacid fruit, and 14 acid fruit. These results would indicate that, as in apples, sweetness tends to be recessive but that the character is controlled by more than one gene.

No study has yet been reported on the transmission of blight resistance. Reimer finds wide variability in blight resistance of individual seedlings of most of the species studied, with occasional blight resistance appearing in all species studied. Crosses of highly

[3] This section is written primarily for students or others professionally interested in breeding or genetics.

resistant Farmingdale with blight-susceptible varieties have resulted in about 25 percent blight-resistant seedlings in the F_1 progenies.

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APPENDIX

TABLE 1.—*Leading pear varieties of the United States*

Variety	Parent species	By whom, where, and how originated
Angouleme	*Pyrus communis*	Wild seedling, Angers, France. Propagated 1808, introduced into the United States before 1830.
Anjou	do	A seedling of Van Mons, according to Bunyard. An old French variety, according to Hedrick. Introduced into the United States 1842.
Bartlett	do	Raised by a Mr. Stair at Aldermaston, Berkshire, England, about 1770. Brought to the United States about 1797.
Bosc	do	A Van Mons variety, 1807. Introduced into the United States in 1832.
Clairgeau	do	Raised by Pierre Clairgeau, Nantes, France, about 1830. Introduced into the United States 1854.
Clapp Favorite	do	Thaddeus Clapp, Dorchester, Mass. Reported Massachusetts Horticultural Society, 1860.
Comice	do	Comice Horticole, Angers, France, 1849. Introduced into the United States in 1850.
Dana Hovey	do	Francis Dana, Roxbury, Mass. Introduced 1854.
Douglas	(*P. communis* × *serotina*) × *P. communis* Kieffer × Angouleme.	O. H. Ayer, Lawrence, Kans., about 1897.
Easter Buerré	*Pyrus communis*	Capucin Monastery, Louvain, Belgium, about 1823; the United States by 1837.
Flemish Beauty	do	Wild pear found by M. Chatillon, Alost, Belgium. Introduced by Van Mons 1818; into the United States about 1830.
Forelle	do	Germany about 1700, the United States 1823.
Garber	*Pyrus communis* × *serotina*.	J. B. Garber, Columbia, Pa., before 1880.
Glou Morceau	*Pyrus communis*	M. Hardenpout, Mons, Belgium, about 1750, the United States about 1820.
Hardy	do	M. Bonnet, Boulogne-sur-Merd., France, about 1820. Introduced into the United States before 1862.

TABLE 1.—*Leading pear varieties of the United States*—Continued

Variety	Parent species	By whom, where, and how originated
Howell	*Pyrus communis*	Thomas Howell, New Haven, Conn., from seed of Jonah planted about 1830.
Idaho	do	Seed planted by Mrs. Mulkey, Lewiston, Idaho, about 1867.
Kieffer	*Pyrus communis* × *serotina*. (Probably sand pear × Bartlett.)	Raised from sand pear seed by Peter Kieffer, Roxborough, Pa., about 1863.
Le Conte	*Pyrus communis* × *serotina*.	Originated in the United States before 1850. Exact history unknown.
P. Barry	*Pyrus communis*	Seedling of Belle Lucrative, raised by B. S. Fox, San Jose, Calif.; fruited 1873.
Pineapple	*Pyrus serotina* × *communis*.	Large seedling tree on plantation of Mrs. B. N. Stuckey, Nesmith, S. C.; possibly brought in from China or Japan.
Seckel	*Pyrus communis*	Chance seedling near Philadelphia about 1800.
Sheldon	do	Premises of Major Sheldon, Huron, N. Y., from seed planted about 1815.
Vermont Beauty	do	Seedling in nursery of B. Macomber, Grand Isle, Vt., about 1880. Hedrick says it is indistinguishable from Forelle.
Wilder Early	do	Chance seedling found by Charles A. Green in Chautauqua Co., N. Y., about 1884.
Winter Nelis	do	Raised from seed by Jean C. Nelis, Mechlin, Belgium, about 1800.

TABLE 2.—*Pear varieties introduced by the New York (State) Experiment Station*

Variety	Parentage	Year crossed	Date introduced	Value
Cayuga	Seckel, open-pollinated	1906	1920	Home and roadside markets.
Clyde	do	1908	1932	Home and local market.
Covert	Bartlett × Dorset	1912	1935	Commercial and export.
Early Seckel	Seckel, open-pollinated	1906	1935	Home and roadside markets.
Gorham	Bartlett × Malines	1910	1923	Commercial market.
Ovid	Bartlett × Dorset	1912	1931	Late winter pear.
Phelps	Winter Nelis × Russet Bartlett	1912	1925	Late home and market.
Pulteney	do	1912	1925	Fall home and market.
Willard	Bartlett × Dorsett	1912	1931	Late winter pear.

TABLE 3.—*Workers on pear breeding in the United States*

Institution	Location of work	Former workers	Present workers
California Agricultural Experiment Station.	Berkeley, Calif.; Davis, Calif.		W. H. Chandler, W. P. Tufts.
Iowa Agricultural Experiment Station.	Ames, Iowa [1]	C. G. Patten	T. J. Maney, B. S. Pickett.
Maryland Agricultural Experiment Station.	College Park, Md	C. P. Close, W. R. Ballard, E. C. Auchter, W. E. Whitehouse.	A. L. Schrader, S. W. Wentworth.
Michigan Agricultural Experiment Station and Department of Agriculture.	South Haven, Mich	W. F. Wight, Don Ward.	Stanley Johnston.
Minnesota Agricultural Experiment Station.	St. Paul, Minn		A. N. Wilcox, W. H. Alderman.
New York State Agricultural Experiment Station.	Geneva, N. Y	S. A. Beach	U. P. Hedrick, Richard Wellington, G. H. Howe.
Oregon Agricultural Experiment Station.	Talent, Oreg		F. C. Reimer.
Tennessee Agricultural Experiment Station.	Knoxville, Tenn	J. A. McClintock	B. D. Drain.
U. S. Department of Agriculture.	Beltsville, Md.; Palo Alto, Calif.	M. B. Waite	J. R. Magness, W. F. Wight.

[1] Prior to 1932, at State Fruit Farm, Charles City, Iowa.

Lists of Pear Material of Special Value for Breeding Purposes

The following institutions have trees of practically all of the *Pyrus* species:
- Arnold Arboretum, Harvard University, Jamaica Plain, Mass.
- California Agricultural Experiment Station, Davis, Calif.
- Southern Oregon Branch Experiment Station, Talent, Oreg.

At the California Station the following varieties not generally available are growing:

Pyrus communis:
- Bollweiller,
- Bonnefond,
- Bordeaux,
- Burkett,
- Caisson,
- Crocker,
- Felix Sahuit,
- Guyot,
- Lady Clapp,
- Large Sugar,
- Longworth,
- Lowe Seedling,
- Marillat,
- Messire,
- Nantes,
- Remy Chatenay,
- Sageret,
- Souvenir de Cronstadt,
- Superfin,
- Thirriott.

P. sinensis:
- Pin Li (P. I. 38263),
- P. I. 40352,
- Nanshi (P. I. 30352).

At the Minnesota Agricultural Experiment Station, St. Paul, Minn., the following material has been tested for hardiness under field conditions, with the results indicated:

1. Completely winter-hardy, tested 10 to 15 years:
   - Minn. Nos. 3 and 4,
   - Minn. Nos. 5, 6, and 7 (seedlings of King Karl × sand pear),
   - Phiel,
   - Russian sand pear,
   - Saponsky.
2. Completely winter-hardy, tested 5 years:
   - Borgman,
   - Cepe Zum Mur (Russia),
   - Patten Nos. 5, 1204, 1205.
3. Completely winter-hardy during tests of 3 to 5 years:
   - Pushken,
   - *Pyrus communis* L., P. I. 47093 et al.,
   - *P. ussuriensis ovoidea* Rehd., P. I. 44051,
   - *P. ussuriensis* Maxim., P. I. 44235, 44237, 44275, et al.,
   - Scandinavian varieties (top-worked branches only):
     - Aldonspare,
     - Esperen Herripare,
     - Furstligt Tafelparon,
     - Grapare,
     - Grev. A. D. Moltke,
     - Johantorp,
     - Juli Dekan,
     - Lübecker Prinzessinpare,
     - Rostbergersmott.
4. Relatively winter-hardy during tests of 3 or more years:
   - *P. betulifolia* Bunge, P. I. 39547,
   - *P brestschneideri* Rehd.,
   - *P. communis* L., P. I. 33207 et al.,
   - *P. phaeocarpa* Rehd., P. I. 32741, 39541, 43185, 44276,
   - *Pyrus* sp., "Favorita," P. I. 33207,
   - *P. ussuriensis* Maxim., P. I. 47094, 55967, 55970,
   - Van Fleet hybrid, P. I. 43443.
5. Relatively hardy, but not completely hardy in Minnesota; tested 5 years or more:
   - Beierschmitt,
   - Chang,
   - Mendel,
   - Parker,
   - Patten Nos. 1200, 1206,
   - Simola,
   - Tait, Nos. 1, 2, and 4.

6. Other species, severely winter-injured but surviving:
   P. calleryana Decne., P. I. 47261,
   P. chinensis,
   P. phaeocarpa Rehd., P. I. 64229,
   Pyrus sp., "Surprise," P. I. 45901,
   Pyrus sp., P. I. 46566, 56012, 64223,
   Pyrus sp., Van Fleet hybrid, P. I. 55805,
   P. ussuriensis Maxim., P. I. 46587.

The New York (State) Agricultural Experiment Station, Geneva, N. Y., has the following pear varieties that are not generally available in the United States:[4]

Admiral Gervais, P. I. 91198,
Alexander Lambré, P. I. 91199,
Ba Li Hsaing,
Barronne de Mello,
Baudry,
Belle Guérandaise, P. I. 91200,
Beurré d'Arenberg (syn. of Glou Morceau),
Beurré Bedford,
Beurré Cadelien,
Beurré Dumont
Beurré Fouqueray,
Beurré Six (P. I. 91201),
Ewart,
Favorita,
Fondante Thirriot,
Gdula,
Hessle,
Lung Li, P. I. 46587,
Koestliche von Charmeau,
Kontoula, P. I. 47227,
Laxton,
Laxton Superb,
Louis Pasteur,
Marie Benoist,
Michurin's,
Ming,
Ne Plus Meuris,
Noveau Poiteau, P. I. 91207,
Nouvelle Fulvie,
Packham Triumph,
Passe Crassane,
Pastoren Birne (syn. of Vicar of Winkfield),
Petite Marguerite, P. I. 91208,
Petre,
President Barabé, P. I. 91209,
Satisfaction,
Soldat Laboureur, P. I. 91210,
Tang Li,
Triomphe de Vienne,
Vergules,
Miscellaneous *Pyrus* species.

At the Southern Oregon Branch Experiment Station, Talent, Oreg., 500 varieties of pears have been collected. Some of these have died of blight and are no longer available. These are listed in Oregon Station Bulletin 214.

[4] Names are substantially as submitted by the station Some are not in full accord with the code of nomenclature.

GRAPE DEVELOPMENT AND IMPROVEMENT

ELMER SNYDER, Pomologist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry [1]

THE present commercial grape industry in the United States has developed along two main lines. On the Pacific coast the industry has depended upon the importation and improvement of varieties of the grape of the Old World, *Vitis vinifera* L., while in the remainder of the country the industry has been based upon the development of the American species indigenous to the region, hybrids of these species, and finally hybrids of native species with *V. vinifera*. On the other hand, the industry in the Old World originated actively from the single species *V. vinifera*. This species has also played a vital part in the improvement of our native grapes. It was known in prehistoric times. Sacred writings and ancient myths and fables extol the value of this grape. Seeds of the grape have been found in the remains of lake dwellings of the Bronze Age in Switzerland and Italy and in the tombs of ancient Egypt. Remains of grape leaves have also been found in calcareous rocks in France, where they were apparently deposited in prehistoric times. It is the belief of botanists that the ancient home of this species was the Caspian Sea region.

DISTRIBUTION AND EARLY HISTORY

FROM its original habitat the grape was carried westward into favorable locations in Africa and Europe and eastward in Asia. The distribution of the species by birds, wind, and water undoubtedly began very early, even before cultivation, and possibly before the existence of man in Asia or Europe. Grape growing was practiced very early in Palestine, and cultural material was transported by the early Phoenician navigators to the countries bordering on the Mediterranean Sea. According to Alphonse de Candolle, records of the cultivation of the grapevine and the making of wine in Egypt go back 5,000 to 6,000 years. Viticulture in Greece was flourishing during the time of Homer and must

[1]The writer wishes to acknowledge the cooperation of the many workers on grape breeding who have supplied the data on which a portion of this report is based. The following have supplied data relative to grape-breeding work in their respective countries: Ing. Fr. Landovsky, State Institute for Horticultural Research, Průhonice, Czechoslovakia; Dr. J. Dufrenoy, Station de Pathologie Végétale, Pont de la Maye, France; Prof. Giovanni Dalmasso, director, Stazione Sperimentale di Viticoltura e di Enologia, Conegliano, Italy; and Prof. Dr. Rudorf, director, Kaiser Wilhelm-Institut für Züchtungsforschung, Müncheberg, Germany. In the United States the following workers have furnished data on their grape-breeding investigations: H. P. Olmo, California Agricultural Experiment Station, Davis, Calif.; H. P. Stuckey, Georgia Experiment Station, Experiment, Ga.; A. L. Schrader, Maryland Agricultural Experiment Station, College Park, Md.; A. N. Wilcox, Minnesota Agricultural Experiment Station, St. Paul, Minn.; Paul H. Shepard, Missouri State Fruit Experiment Station, Mountain Grove, Mo.; Richard Wellington, L. M. Van Alstyne, and B. R. Nebel, New York (State) Agricultural Experiment Station, Geneva, N. Y.; F. E. Gladwin, Vineyard Substation of the State station, Fredonia, N. Y.; S. H. Yarnell, Texas Agricultural Experiment Station, College Station, Tex.; Fred W. HofMann, Virginia Agricultural Experiment Station, Blacksburg, Va.; C. A. Magoon and I. W. Dix, U. S Horticultural Station, National Agricultural Research Center, Beltsville, Md.; and Charles Dearing, Coastal Plain Branch Station, Willard, N. C.

have been known before his time. The Romans doubtless gained their knowledge of grape growing and the art of wine making from the Greeks. For a time the Romans seemed to prefer the Grecian product, and not until about the first century of the Christian Era did Italian wines begin to have a favorable reputation in their own region.

In the meantime French viticulture was originating in the vicinity of what is now Marseilles and spreading up the valley of the Rhone. In the second century A. D. it had spread along the banks of the Rhine. From a centralized beginning the growing of *Vitis vinifera* has gradually spread until at the present time it is grown commercially in parts of Europe, Asia, Africa, Australia, North America, and South America. Grape growing is practiced in the Northern Hemisphere mainly between 20° and 51° N. latitude, and varieties of *Vitis vinifera* are found in many of the countries bounded by these parallels. The most northern range of the varieties of *Vitis vinifera* is in the grape area of northern Germany, while the southern range extends into India. In the Southern Hemisphere, including Australia, South Africa, and South America, grape growing is carried on mainly between 20° and 40° S. latitude.

Introduction of Old World Grapes Into the United States

American colonists at a very early period understood the culture of the vine. The abundance of native grapevines along the Atlantic coast attracted their attention, but the first attempts, made early

THE *major portion of the grape-breeding work conducted by public institutions has been to improve quality, which is an elusive factor. The quality of our native varieties has been improved by crossing them with the best varieties of the European grape. Improvements in type of cluster and type of berry have been made by combining different native species. Rootstocks have been developed through hybridization which have suitable resistance to phylloxera, the deadly insect enemy of the grape, and are adapted to various soil types. Thus real progress has been made. But continued improvement is possible, and the results so far indicate that it can be obtained through hybridization. Grape breeding is relatively new, and there is need for more information on the inheritance of such characteristics as size, quality, seedlessness, cold hardiness, disease and insect resistance, and adaptability to environment. Rich collections of species and varieties are available as breeding material to bring about the further improvements that will result in increased consumption of grapes.*

in the seventeenth century, were with the vinifera or European grape. In 1619–21 the London Co., actively urging the culture of the vinifera grape as a source of revenue, brought French vine workers and collections of the best vinifera grape varieties of France to the settlements in Virginia. The Colonial Assembly was also active at the same time in encouraging and even ordering the care and cultivation of the vine. Similar attempts were made in the various colonies from New England to Georgia from 1619 to the beginning of the Revolutionary War.

Much has been written concerning these early attempts at growing vinifera grapes in eastern United States. The reports can be briefly summarized. The first year or two the vines gave considerable promise, then disease and insects appeared, resulting in dead vines and finally an abandoned vineyard. From present experience it would appear that lack of resistance to cold, insects, and disease in the northern regions, and susceptibility to disease and insect injury in the southern regions, were the factors responsible for the general failure of vinifera grape culture in eastern United States.

While failures were being recorded with vinifera grapes along the Atlantic coast, a start in their culture was being made on the Pacific slope in California. The Mission Fathers, going northward from Mexico, established the San Diego Mission in 1769. They brought grape material with them to plant at the various missions established from San Diego to Sonoma. The first plantings made were of a variety that became known as the Mission and represents earliest successful culture of vinifera grapes in the United States. Very little further development took place in California until after 1850. An essay by Col. Agostin Haraszthy on grape growing and wine making, published in 1858 and given wide circulation by the California State Agricultural Society, so stimulated viticulture in the State that 20,000,000 vines had been planted by 1862. Cuttings and rooted vines, including many of the better known varieties then grown in Europe, were introduced into California and distributed to growers. During the following years commercial grape growing, based entirely on vinifera grapes, developed rapidly. Production increased from 11,000 tons in 1869 to 360,000 in 1899, 1,827,000 in 1929, and 2,065,000 tons in 1935. Vinifera grape culture has also spread to other Western and Southwestern States. In favorable locations in Idaho, Washington, Oregon, Nevada, Arizona, Utah, New Mexico, and Texas, vinifera grapes prove profitable for local sale and, in special southern locations, for early commercial shipments.

Development and Early Improvement of American Native Grapes

After many failures with varieties of *Vitis vinifera* in the East, the native species were finally considered to be the best basis for an eastern grape industry.

Out of a planting of vinifera grapes made by the Kentucky Vineyard Society shortly after 1802, near the present site of Vevay, Ind., several varieties resisted unfavorable conditions better than others. One of these was called the Cape grape by John James Dufour II. This grape was later supposed to be identical with Alexander, a native

American vine, which had been planted in some way among the vinifera varieties. Later, from 1806 on, this native grape became generally distributed and was grown with apparent success. Grape authorities later considered the Alexander an offshoot of *Vitis labrusca* L., with a possibility of some vinifera species in its parentage. It probably originated along the banks of the Schuylkill in Pennsylvania, and its history antedates the Revolutionary War.

The next incentive to native grape growing came with the introduction of the Catawba variety. Its origin is uncertain. There is evidence that it originated in North Carolina. In 1819 John Adlum (1759–1836) obtained cuttings of the Catawba from a cultivated vine in Maryland for extensive nursery propagation in the District of Columbia. The cuttings of the variety were widely distributed by Adlum and some were sent to Nicholas Longworth (1783–1863) in Ohio, who became greatly impressed with it. During the period from 1825 to 1850 this variety, as well as Isabella and others less well-known, was planted in widely separated parts of the Eastern States. These two varieties were predominant until the introduction of the Concord, which originated from a chance seedling grown by Ephraim Wales Bull (1805–95), of Concord, Mass. The seed was planted in 1843 and produced fruit in 1849. The grape was named Concord and introduced in the spring of 1854. The Concord grew rapidly in popularity and its culture had spread to Missouri by 1855, 1 year after its introduction.

The improved varieties of native grapes introduced between 1800 and 1850 were principally chance seedlings or selections from wild native species. Since 1850 many men have been interested in grape breeding for the improvement of our native species.

Native species of *Vitis* are found in all parts of the United States. The fruit of many of them is of little direct value, but even the species producing poor fruit may have characters of value for hybridization and plant breeding. Some have been the source of our cultural varieties, while others are very valuable as stocks resistant to phylloxera and the root knot nematode. Table 1 indicates the main grape species that have been used in breeding work.

TABLE 1.—*Grape species possessing special breeding qualities*

Species, common name, and natural range	Character of vine	Resistance to— Phylloxera [1]	Cold [2]	Heat [2]	Wet [2]	Dry [2]	Qualities for breeding
Vitis aestivalis Michx; summer grape. New England to Georgia and westward to the Mississippi River.	Vigorous, climbing, leaves large, 20 cm, 3- to 5-lobed	14	VG	G	F	G	Resistance to fungus diseases; high sugar percentage; suitable wine properties; possible table use if crossed with large-berried varieties.
V. aestivalis var. *bourquiniana* Bailey (*V. bourquiniana* Muns.); Bourquin grape. Origin doubtful; adapted to Southeastern States.	Vigorous, climbing; leaves large, 3- to 5-lobed.	---	F	G	F	G	Vigor; disease resistance; productiveness; colored juice.

TABLE 1.—*Grape species possessing special breeding qualities*—Continued

Species, common name, and natural range	Character of vine	Resistance to— Phylloxera [1]	Cold [2]	Heat [2]	Wet [2]	Dry [2]	Qualities for breeding
V. berlandieri Planch.; Spanish grape, winter grape. Texas and northern Mexico.	Medium vigor, slender; leaves medium, 10 cm, 3-to 5-lobed.	19	F	G	F	G	Rootstock resistance to phylloxera; ability to grow on strong, limy soils.
V. candicans Engelm.; mustang grape. Mainly Texas, parts of Arkansas, Oklahoma, Louisiana, and Mexico.	Very vigorous, high climbing, leaves medium, nonlobed to 3-lobed.	15	F	G	F	G	Vigor for rootstock; easily hybridized; adapted to black limestone lands; large-berried fruit for wild vine.
V. champini Planch.; Champin grape. Mainly Texas.	Very vigorous, climbing; leaves medium, 10-12 cm, nonlobed to 3-lobed.	15	F	G	G	G	Vigor for rootstock; healthy foliage; wide adaptability; large-berried fruit.
V. cordifolia Lam.; frost grape. Wide range, from Great Lakes to Florida.	Vigorous, climbing; leaves medium, 10 cm.	18	G	G	G	G	Vigor; phylloxera resistance; wide natural range.
V. labrusca L.; fox grape. New England to northern Georgia, westward to Indiana, and bordering the Ohio River.	Medium vigor, climbing; leaves large, nonlobed to slightly lobed.	5	VG	F	F	F	Cold resistance; large-berried fruit; strong distinctive flavor.
V. linsecomii Buckl.; pinewoods grape, post-oak grape. Texas, parts of Louisiana, Oklahoma, Arkansas, and Missouri.	Vigorous, bushy to climbing; leaves very large, 3- to 5-lobed.	14	F	G	G	VG	Vigor; disease resistance; large clusters and berries; strong flavor.
V. longii Prince; Longs grape, bush grape. Parts of Arkansas, Oklahoma, Texas, New Mexico, and southeastern Colorado.	Very vigorous, bushy to climbing; leaves large, 3- to slightly 5-lobed.	14	G	G	VG	G	Vigor; phylloxera resistance; easy rooting of cuttings; vinous flavor.
V. monticola Buckl.; sweet mountain grape. Texas.	Medium vigor, slender, climbing; leaves small, nonlobed to slightly 3-lobed.	18	G	F	F	G	Phylloxera resistance; health of foliage; fruit medium to small.
V. rotundifolia Michx.; muscadine grape. Potomac River to Florida and west to eastern Texas.	Vigorous, slender, climbing; leaves small, not lobed.	20	F	G	F	G	Disease-resistant vine and fruit; special fruit flavor.
V. rupestris Scheele; sand grape. Southern Missouri and Illinois, Kentucky, Tennessee, Oklahoma, and eastern and central Texas to the Rio Grande.	Very vigorous, bushy, rarely climbing; leaves small, mostly nonlobed.	19	F	G	G	G	Phylloxera resistance; easy propagation; vigorous.
V. vulpina L.; riverbank grape. Canada to Texas and west to Great Salt Lake; wide range.	Vigorous, slender, moderately climbing; leaves large, mostly nonlobed, to slightly 3-lobed.	19	VG	F	G	F	Phylloxera resistance; cold resistance; easy propagation.
V. vinifera L.; European grape, wine grape. Introduced species.	Medium to strong vigor, bushy to climbing; leaves mostly 3- to 5-lobed, occasionally 7-lobed.	1	F	VG	F	G	Productiveness; high quality; easy propagation; some seedlessness.

[1] Ratings under phylloxera resistance are from 1 indicating greatest susceptibility to 20 indicating almost complete resistance.
[2] Symbols for resistance to cold, heat, wet soil, and drought are: VG=very good. G=good. F=fair.

One of the native species used extensively for breeding is *Vitis labrusca*, the fox grape. From chance seedlings of this species came Catawba and Concord, though they may also possibly have some

V. vinifera in their parentage. Through early hybridization work a number of popular varieties were obtained from *V. labrusca* crossed with *V. vinifera.* One of the earliest grape breeders in this country to utilize this cross was Edward Staniford Rogers (1826–99), of Massachusetts (fig. 1). Although engaged primarily in the shipping business with his father, he became interested in horticulture and conducted his experiments in grape hybridization in a garden on a city lot back of his home. In originating the group known as Rogers hybrids he used a large-fruited red labrusca known as Carter and fertilized the blossoms with pollen of two vinifera varieties, Black Hamburg and White Chasselas. From these crosses, made in 1851, he obtained about 150 seeds, which eventually produced 45 fruiting vines of high quality. These came into bearing between 1856 and 1858 and were numbered from 1 to 45 by Rogers. They were widely distributed, and some were finally named. Rogers continued his work and recrossed varieties already produced, but none of the later seedlings was promising enough to be introduced. This early work of Rogers indicated the value of *V. vinifera* in hybridizing to improve the quality of the native fruit. The Agawam variety is one of his main contributions that is still grown.

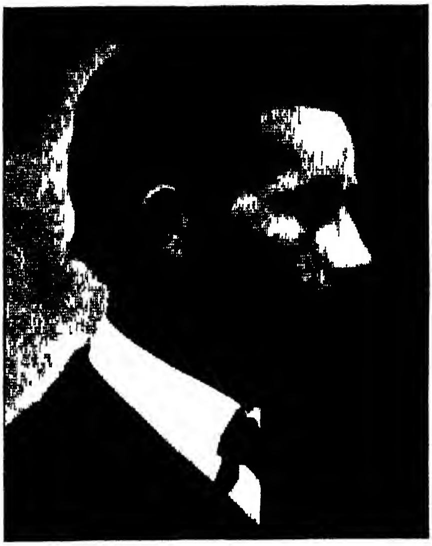

Figure 1.—**Edward Staniford Rogers, of Massachusetts, a pioneer in grape hybridization.**

Contemporary with Rogers were many other men who introduced hybrid varieties of their own breeding. Only a few of these can be mentioned here.

Andrew Jackson Caywood (1819–89), a nurseryman and fruit grower, became interested in grape breeding in New York. Little record of his methods remains. He differed from other grape breeders of his time, however, in concentrating on second-generation hybrids. The Dutchess represents one of his most important named varieties.

Charles Arnold (1818–83), of Canada, produced many seedlings. Since he lived near the northern limits of grape culture, he was interested mainly in producing cold hardiness in seedlings of high quality. His crosses were mainly a combination of *Vitis labrusca, V. vulpina* (the riverbank grape), and *V. vinifera.* His productions proved hardy under severe climatic conditions but were more or less susceptible to disease. Canada and Othello are two of his named varieties.

George W. Campbell (1817–98) conducted his grape-breeding work in Ohio and raised many seedlings. He used varieties mainly of *Vitis labrusca* and *V. vinifera* and to some extent *V. aestivalis* var.

bourquiniana (Munson) Bailey. Campbell Early represents his main contribution to present-day viticulture.

Louis Suelter, of Carver, Minn., carried on most of his hybridizing work between 1870 and 1884. Previous to this time he had grown many seedlings of the wild grape, *Vitis vulpina*. One of these seedlings appeared to blossom earlier and develop fruit color earlier than others. By crossing this with Concord as the pollen parent, four seedlings were produced and named Beta, Dakota, Monitor, and Suelter. These are reported to be hardy for the more northern and northwestern parts of the country, and they illustrate the use of *V. vulpina* in obtaining cold-resistant varieties.

James H. Ricketts (1818–1915), who conducted a bookbinding business in Newburgh, N. Y., became interested in grape improvement, and one of his first productions was Raritan. In order to utilize vinifera varieties to cross with native grapes he constructed a glasshouse for their culture. While his seedlings were not very vigorous, because of their large proportion of vinifera parentage, they were characterized by high quality and large cluster and berry. His crosses were mostly *Vitis labrusca* and *V. vinifera*. Some however, were complex hybrids, containing in addition either *V. aestivalis* (the summer grape) × *V. aestivalis* var. *bourquiniana* or *V. vulpina* parentage. Some of his named varieties include Downing, Empire State, and Jefferson.

Figure 2.—Thomas Volney Munson, of Texas, who did notable work in the botanical study and hybridizing of grapes. He originated and introduced many superior hybrid varieties, including varieties of the bunch type especially suitable for southern conditions.

Thomas Volney Munson (1843–1915, fig. 2) conducted most of his breeding work with grapes at Denison, Texas. The region in which he lived is rich in native species. Munson gave much of his time to the botanical study of grape species as well as to breeding and cultivating new varieties. In 1909 he published a summary of his extensive work with grape species, breeding, and the testing of grape varieties (*6*).[2] His work was largely instrumental in producing grape varieties of the bunch type suitable for southern conditions, where most of our varieties of northern parentage fail. Of particular interest and special value was his use of the native species *Vitis linsecomii*, the pinewoods grape, in the origination of hybrid varieties. By combining and selecting the vigorous, healthy native species Munson was able to originate fruiting varieties that are productive, vigorous, and better in

[2]Italic numbers in parentheses refer to Selected References on Grape Breeding, p 655.

fruiting qualities than the parental types. More hybrid grape varieties have been originated and introduced through his efforts than by any other agency in the United States.

Other grape breeders who have contributed some of our better known varieties include Joseph Backman, Hermann Jaeger, Jacob Moore, and Jacob Rommel.

Table 2 gives the parentage and origin, so far as they are known, of a number of the more important native American grape varieties. Some of the varieties that originated as chance seedlings, including Catawba, Concord, and Delaware, are among the most important commercial varieties at the present time. However, when varieties were needed for a specific purpose, such as hardiness, insect resistance, or improved quality, controlled crossing became necessary. The better known varieties are marked with an asterisk, and these can usually be obtained from some of the many commercial nurseries. Others are included as a partial list of varieties available for breeding purposes in State or Federal experimental plantings.

TABLE 2.—*Parentage and origin of American native grape varieties*

[An asterisk (*) denotes the better known varieties.]

Variety	Color	Stamens	Species parentage [1]	Originated or introduced by—	Date	State or country of origin
Agawam*	Red	Upright	Lab., Vin	E. S. Rogers	1855	Massachusetts.
Arkansas	do	do	Lab	Joseph Hart	1893	Arkansas.
Bacchus	Black	do	Vulp., Lab	J. H. Ricketts	1879	New York.
Banner	Red		Lab., Vin., Bourq.	Joseph Backman	1898	Arkansas.
Barry	Black	Reflex	Lab., Vin	E. S. Rogers	1855	Massachusetts.
Beacon*	do	Upright	Linc., Lab	T. V. Munson	1886	Texas.
Berckmans	Red	do	Vulp., Lab., Bourq.	A. F. Wylie	1871	South Carolina.
Beta*	Black	do	Vulp., Lab	Louis Suelter	1881	Minnesota.
Brighton*	Red	Reflex	Lab., Vin	Jacob Moore	1872	New York.
Brilliant*	do	Upright	Lab., Vin., Bourq.	T. V. Munson	1883	Texas.
Caco*	do	do	Lab., Vin	J. T. Lovett	1901	New Jersey.
Campbell Early*	Black	do	do	G. W. Campbell	1892	Ohio.
Canada	do	do	Vulp., Lab., Vin	Charles Arnold	1860	Canada.
Carman*	do	do	Linc., Lab., Vin., Bourq.	T. V. Munson	1892	Texas.
Catawba*	Red	do	Lab., Vin	John Adlum	1823	District of Columbia.
Champanel	Black	do	Champ., Lab	T. V. Munson	1893	Texas.
Champion*	do	do	Lab	Uncertain	1870	New York.
Charles A. Green	White	do	do	F. W. Loudon		Wisconsin.
Clinton*	Black	do	Vulp., Lab	L. B. Langwell	1835	New York.
Colerain	White	Reflex	Lab	David Bundy	1880	Ohio.
Columbian Imperial.*	Black	Upright	Lab., Vulp	J. S. McKinley	1885	Do.
Concord*	do	do	Lab	Ephraim W. Bull	1849	Massachusetts.
Creveling	do	Reflex	Lab., Vin	F. F. Marceron	1857	Pennsylvania.
Croton	White	Upright	Lab., Vin., Bourq	S. W. Underhill	1865	New York.
Cynthiana*	Black	do	Aest., Lab	W. M. Prince	1850	Arkansas.
Dakota	do	do	Vulp., Lab	Louis Suelter	1881	Minnesota.
Delaware*	Red	do	Lab., Vin., Bourq.	A. Thompson	1881	Ohio.
Diamond*	White	do	Lab., Vin	Jacob Moore	1870	New York.
Diana	Red	do	do	Diana Crehore	1884	Massachusetts.
Downing	Black	do	do	J. H. Ricketts	1865	New York.
Dracut Amber	Red	do	Lab	A. Clement	1855	Massachusetts.
Dutchess*	White	do	Lab., Vin., Bourq., Aest.	A. J. Caywood	1868	New York.
Eaton	Black	do	Lab	M. C. Eaton	1879	New Hampshire.
Ellen Scott*	Red	do	Linc., Lab., Vin	T. V. Munson	1902	Texas.
Elvira*	White	do	Vulp., Lab., Vin	Jacob Rommel	1863	Missouri.
Empire State	do	do	Lab., Vulp., Vin	J. H. Ricketts	1874	New York.
Eumelan	Black	Reflex	Lab., Vin., Aest	— Thorne	1847	Do.
Fredonia*	do	Upright	Lab	N. Y. Agr. Expt. Sta.	1915	Do.

[1] Abbreviations are used for species as follows: Aest. for *Vitis aestivalis;* Bourq. for *V. aestivalis* var. *bourquiniana;* Champ. for *V. champini;* Cin. for *V. cinerea;* Lab. for *V. labrusca;* Linc. for *V. linsecomii;* Rup. for *V. rupestris;* Vin. for *V. vinifera;* Vulp. for *V. vulpina.*

TABLE 2.—*Parentage and origin of American native grape varieties*—Continued

Variety	Color	Stamens	Species parentage	Originated or introduced by—	Date	State or country of origin
Goethe	Red	Reflex	Lab., Vin	E. S. Rogers	1855	Massachusetts.
Golden Muscat	White	Upright	Vin., Lab	N. Y. Agr. Expt. Sta.	1916	New York.
Governor Ross	do	do	Lab., Vin	T. V. Munson	1894	Texas.
Green Early	do	do	Lab	O. J. Green	1887	New York.
Grein Golden	do	Reflex	Vulp., Lab	Nicholas Grein	1881	Missouri.
Hartford	Black	Upright	Lab., Vin	P. W. Steel	1849	Connecticut.
Herbemont*	Red	do	Bourq	Indefinite		South Carolina.
Herbert	Black	Reflex	Lab., Vin	E. S. Rogers	1855	Massachusetts.
Iona*	Red	Upright	do	C. W. Grant	1855	New York.
Isabella*	Black	do	do	— French	1816	Do.
Ives*	do	do	Lab., Aest	H. Ives	1840	Ohio.
Jefferson	Red	do	Lab., Vin	J. H. Ricketts	1888	New York.
Lady Washington.	White	do	do	do	1878	Do.
Lenoir*	Black	do	Bourq	Indefinite		
Lindley	Red	Reflex	Lab., Vin	E. S. Rogers	1855	Massachusetts.
Louisiana	do	Upright	Bourq	M. Theard	1860	Louisiana.
Lucile*	do	do	Lab	J. A. Putman	1890	New York.
Lutie	do	do	do	L. C. Chisholm	1865	Tennessee.
Manito	Black	do	Linc., Rup., Lab., Vin., Bourq.	T. V. Munson	1899	Texas.
Martha	White	do	Lab., Vin. (?)	S. Miller	1864	Missouri.
Mills	Black	do	Vin., Lab	W. H. Mills	1870	Canada.
Moore Early*	do	do	Lab	J. B. Moore	1871	Massachusetts.
Muench*	do	do	Linc., Bourq	T. V. Munson	1886	Texas.
Niagara*	White	do	Lab., Vin	Hoag and Clark	1872	New York.
Nitodel	Black	do	Cin., Lab., Vin., Bourq.	T. V. Munson	1902	Texas.
Noah	White	do	Vulp., Lab	Otto Wessenzicher	1873	Illinois.
Ontario *	do	do	Lab., Vin., Aest	N. Y. Agr. Expt. Sta	1908	New York.
Oriental	Red	do	Lab., Vin	M. B. White	1883	Massachusetts.
Perkins	do	do	do	J. Perkins	1830	Do.
Pierce*	Black	do	do	I. B. Pierce	1903	California.
Pocklington	White	do	Lab	John Pocklington	1870	New York.
Portland*	do	do	do	N. Y. Agr. Expt. Sta.		Do.
Poughkeepsie	Red	do	Lab., Vin., Bourq.	A. J. Caywood	1880	Do.
Rebecca	White	do	Lab., Vin.	E. M. Peak	1856	Do.
Ripley	do	do	Lab., Vin., Aest	N. Y. Agr. Expt. Sta.	1912	Do.
Rommel	do	do	Vulp., Lab., Vin	T. V. Munson	1885	Texas.
Salem	Red	Reflex	Lab., Vin	E. S. Rogers	1855	Massachusetts.
Secretary	Black	Upright	Vulp., Lab., Vin	J. H. Ricketts	1867	New York.
Sheridan	do	do	Lab., Vin	N. Y. Agr. Expt. Sta.	1921	Do.
Suelter	do	do	Vulp., Lab	Louis Suelter	1883	Minnesota.
Sunrise	Red	do	Lab., Vin., Bourq.	J. Backman	1897	Arkansas.
Vergennes*	do	do	Lab	W. C. Green	1874	Vermont.
Westfield	Black	do	Lab., Vin	N. Y. Agr. Expt. Sta.	1922	New York.
Winchell*	White	do	Lab., Vin., Aest	J. A. Clough (?)		Vermont.
Wine King	Black	do	Aest., Linc., Rup	T. V. Munson	1898	Texas.
Worden*	do	do	Lab	Schuyler Worden	1863	New York.
Wyoming	Red	Reflex	do	S. J. Parker	1870	Do.

TECHNIQUE OF BREEDING

STRUCTURE OF GRAPE BLOSSOMS

TO UNDERSTAND the technique of breeding new grape varieties, some knowledge of the floral parts (fig. 3) is necessary. The blossoms of *Vitis* are arranged in a pyramidal, loosely branched cluster known as a panicle. In the wild state some vines may bear only male or staminate flowers, while others bear perfect or hermaphrodite flowers that have both stamens and pistils. American native species bear male flowers and hermaphrodite flowers on separate vines, while most European vines of *Vitis vinifera* bear only hermaphrodite flowers. The male flowers (fig. 3, *A*) differ from the hermaphrodite flowers in bearing well-developed stamens and only an incompletely developed pistil, which has no style or stigma and only a very small ovary, the ovules of which cannot be fertilized. The pollen grains of the male

flowers will germinate and can fertilize flowers that have a normally developed pistil.

The hermaphrodite blossoms range from flowers having reflexed, very poorly developed stamens (fig. 3, *B*) to perfect flowers with upright stamens (fig. 3, *C*). Varieties with reflex stamens usually do not set fruit, or set only very loose clusters, unless they are cross-pollinated, either naturally or artificially. Each individual perfect flower normally bears five stamens although the number may vary on the same flower cluster from four to eight. The stamen consists of the filament tipped by the anther containing a pair of pollen sacs. The stamens surround the fruit-producing part of the flower known as the pistil, which is made up of the stigma, a slender-necked style, and an enlarged ovary. The ovary contains the ovules which develop into seeds after fertilization has taken place.

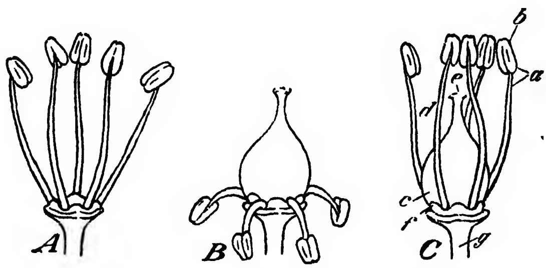

Figure 3.—Grape flower parts. *A*, Male flower. *B*, Flower with reflex stamens. *C*, Flower with upright stamens: *a*, Filament; *b*, anther; *c*, ovary; *d*, style; *e*, stigma; *f*, nectar gland; *g*, pedicel.

Previous to opening, these flower parts are enclosed in a cap-shaped united corolla (fig. 4, *A*). At the time of blossoming, the corolla is shed by becoming loosened at the base and coming off like a cap (fig. 4, *B*). When the flowers are in full bloom, each pollen sac of the anthers splits and sheds the pollen, which is in the form of small, ellipsoid, yellow grains. When moistened the grains take on a globular form. If examined microscopically, it can be noted that the pollen grain is enclosed in a cell wall with three thin-walled bands extending around the grain from pole to pole. In the middle of each of these bands is located a germinal pore through which the pollen tube will subsequently develop.

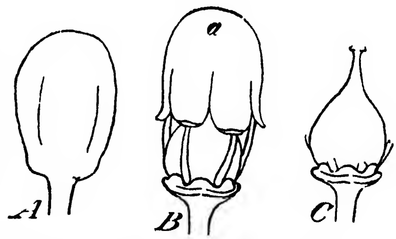

Figure 4.—*A*, Grape flower bud. *B*, Flower bud partly opened; *a*, corolla or cap. *C*, Emasculated flower.

The pollen grains are deposited on the stigma through natural or artificial means. If the stigma is receptive and the pollen grain viable, the pollen germinates and the pollen tube grows through the style, reaches the ovary, and enters an ovule through a small passage between its outer and inner coverings known as the micropyle. Fertilization then takes place by fusion of a sperm nucleus from the pollen tube with the egg nucleus in the ovule. The fertilized ovules become the grape seeds, and the ovary develops into the fruit or grape berry.

Method of Hybridizing

. The steps used in the actual hybridizing of grapes by various workers are more or less similar. After selection of the parent varieties, the flower clusters of the male or pollen parent are enclosed on the vine in sacks of paper, cellophane, or other material before any of the individual flowers have opened. This prevents contamination of the desired pollen by the pollen of other nearby varieties. As the blossoms open, the pollen remains within the sack and can be carried directly to the variety to be pollinated or gathered into a suitable container for future use.

The anthers are removed from flowers of the female parent before any pollen has been shed, and the emasculated cluster is enclosed in a bag to prevent the entrance of foreign pollen. At the time of pollination, the pollen from the selected male parent is brushed over the stigmas of the emasculated seed parent. When the fruit is ripe, the seeds are collected, washed, cleaned, and stored for future planting.

Time can be saved by germinating the seeds in a greenhouse. The young seedlings are usually transplanted to pots, cans, or a coldframe for growing one season before they are planted in the field for fruiting tests. The seedlings need some protection the first summer, varying with the climatic conditions under which they are grown. For field trial they are usually planted closer than in commercial vineyards, mainly to conserve space. From reports received, the distances vary from 6 inches to 4 feet in the row, with rows 5 to 12 feet apart. Fruiting may take from 2½ to 4½ years after the seedlings were set in vineyard form, or from 3½ to 5½ years from the time the seed was planted.

Recently a procedure that hastens the fruiting of grape seedlings has been followed at the United States Experiment Vineyard, Fresno, Calif. Grape seeds from controlled crosses in breeding work are planted in flats and started under greenhouse conditions about February 1. The seedlings are transplanted to 1-gallon cans after three or four true leaves are formed. During May and early June of the same season these seedlings attain a growth of from 12 to 16 inches. At this time three or four buds from the basal part of the seedling shoot can be obtained which are suitable for T budding. These seedling buds are T-budded into vigorous shoots of rootstocks or of bearing vines that are growing in vineyard form. With special care and training the seedling buds can be forced into growth. By the end of the first growing season, shoots from 6 to 12 feet long can be developed. At pruning time a cane 3 to 4 feet long can be left for next season's fruiting wood. At the Fresno station ripe fruit has been picked in August, 18 months from the time the seeds were planted in flats. This method saves at least 2 or 3 years compared with the usual method of fruiting grape seedlings. While it may not serve as a test of the commercial merits of a seedling, it does serve to determine many qualities such as color, shape, size, and flavor of the fruit. As with all breeding work, selection of desirable seedlings is necessary. A number of vines of each seedling must be grown and observations made of its commercial possibilities under various soil and climatic conditions before it can be introduced for commercial culture.

PRESENT GRAPE-BREEDING WORK IN THE UNITED STATES

In recent years hybridization of grape varieties and species has been actively carried on at Federal and State experiment stations. Most of the expansion has taken place since 1900, although a few of the State stations were engaged in grape breeding previous to that time. The most active interest has been evidenced since 1920. A recent survey indicates that in addition to the grape-breeding program of the Department the following State stations are conducting grape-breeding work: California, Georgia, Maryland, Minnesota, Missouri, New York, South Dakota, Texas, and Virginia.

The principal objectives have been improvement in fruit quality, productivity, disease resistance, and adaptability to soil and climatic conditions. The work is being carried on with three distinct types that are of commercial importance in the United States—the American native bunch grapes, the muscadine grapes, and the European or Old World grapes.

Native Bunch Grapes

The native bunch grapes have been developed from various native species, in many cases with the infusion of the European grape through natural or controlled hybridization. The species from which the varieties of this group have been derived rank in importance in the following order: *Vitis labrusca*, *V. vinifera*, *V. aestivalis*, *V. linsecomii*, *V. vulpina*, *V. aestivalis* var. *bourquiniana*, *V. champini*, *V. rupestris*, *V. cinerea*. This group, represented commercially by such varieties as Beacon, Catawba, Concord, Cynthiana, Delaware, Iona, Lenoir, Niagara (fig. 5), and others of lesser importance, is grown, at least for home consumption, in every State in the Union. Commercial production is principally in the North Atlantic States, the Great Lakes region, the Central States, and to a lesser extent in the South and in the Pacific Northwest. They are used for table, local markets, shipment for some distance, unfermented juice, and wine. The vines of this type are characterized by medium to vigorous growth; the leaves are medium to large, three- to five-lobed or entire; the tendrills are forked; and the fruit clusters are small to above medium in size. The individual berries of different varieties vary in outline from globular to ovoid. The skin separates easily from the pulp, while the seeds are firmly retained in the pulp. The varieties that have *V. labrusca*, or fox grape, parentage are characterized by what is called a foxy flavor, which is very important in the manufacture of unfermented juice.

The trend of grape breeding with the native bunch grapes has been to improve quality by crossing with varieties of *Vitis vinifera*. This has been successfully done by the New York (State) Agricultural Experiment Station, which has introduced 21 named seedlings for commercial trial. The northern species, *V. labrusca* and *V. vulpina*, have been utilized by the Minnesota and South Dakota Stations to develop varieties with cold hardiness for the northern regions. Size of berries has been increased by the use of *V. labrusca*. Cold hardiness and adaptability have been developed by the use of *V. vulpina*. Thirty-two named seedlings have been introduced by the South

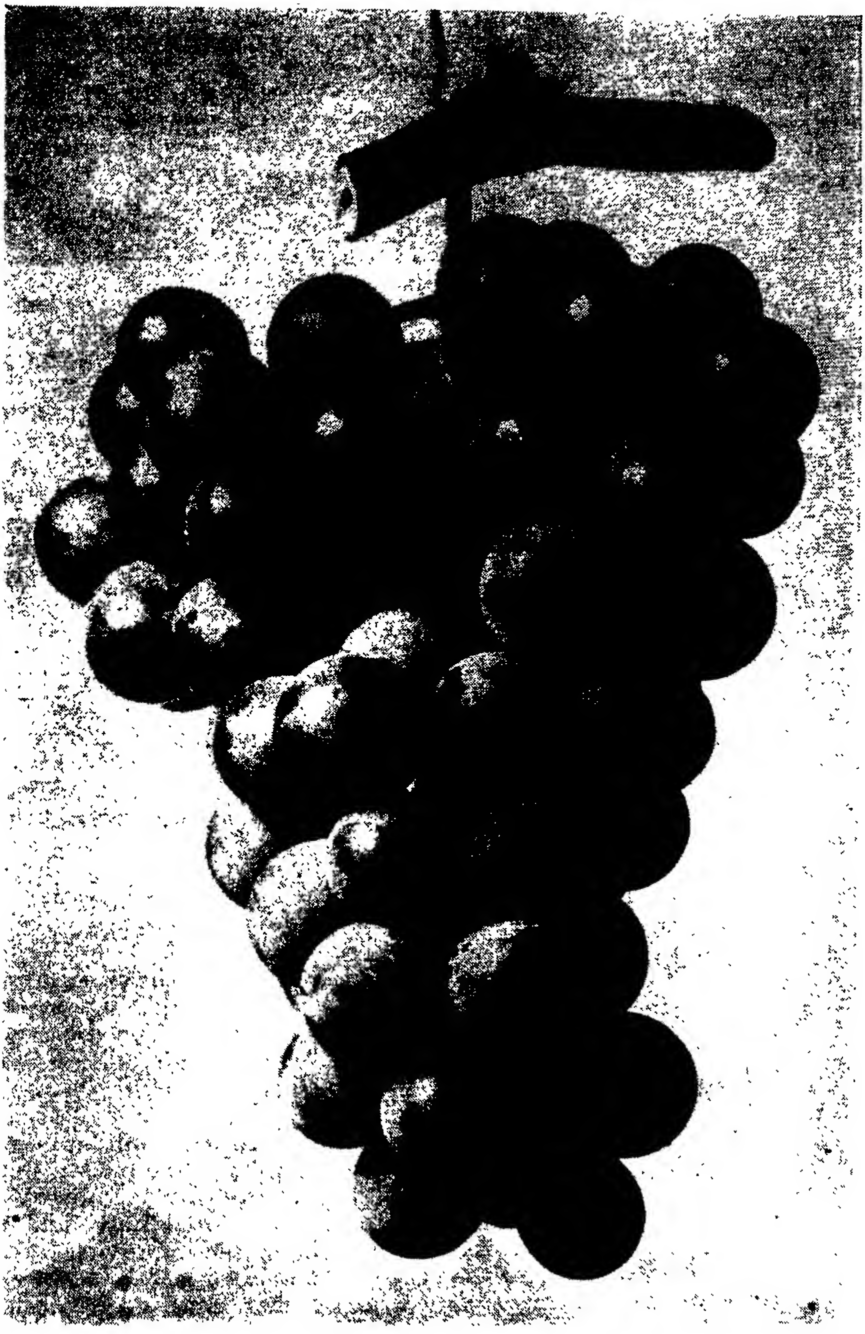

Figure 5.—The Niagara, one of the high-quality grape varieties developed from American species.

Dakota Station. The stations of Maryland, Missouri Texas, and Virginia, and the United States Department of Agriculture at Beltsville, Md., are conducting grape-breeding work to improve the quality and adaptability of the native bunch-grape types by crossing varieties containing labrusca and vinifera parentage with varieties developed from more southern species, such as *V. aestivalis*, *V. aestivalis* var. *bourquiniana*, *V. champini*, *V. linsecomii*, and *V. rupestris*.

Desirable Objectives in Breeding American Bunch Grapes

In the United States the desirable objectives in breeding the American bunch grapes vary with the regions in which they are grown, and regional needs must be studied separately. Three main regions are involved: (1) The North Atlantic States, the grape-growing areas along the Great Lakes, and the North Central States; (2) the Southern States; and (3) the northern Great Plains.

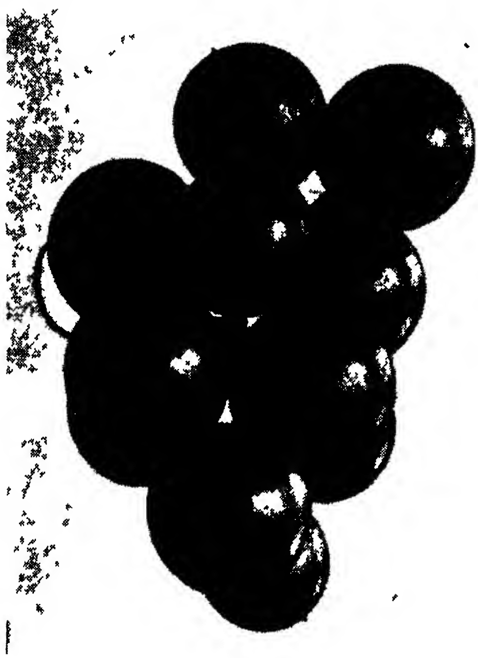

Figure 6.—A typical cluster of muscadine grapes, Scuppernong variety.

In the first region it would seem desirable, in the case of table grapes, to combine increased production with increased size of cluster and berry. In quality, the strong flavor of the labrusca may be ameliorated by the addition of the rich vinous flavor of the vinifera. The skin should be more edible and the flesh more melting than is the case with the Concord type if these qualities can at the same time be combined with improved shipping and handling qualities. The sugar content could be increased and the acidity adjacent to the seeds decreased. The seeds should separate readily from the pulp. It may not be too much to hope that the seeds can at some future time be entirely eliminated. In the case of varieties for unfermented juice, increased productiveness, a more highly colored juice, and a more melting pulp would seem desirable. Desirable improvement in varieties for wine varies with the type of wine. In general, increased sugar content, more juice production, and earlier maturity are desirable objectives. The development of a more vigorous, hardy, disease-resistant, and insect-resistant root system would materially aid the industry as a whole.

In the second region, the Southern States, important consideration should be given to resistance to disease and insect injury, principally downy mildew (*Plasmopara viticola* (Berk. and Curt.) Berl. and DeToni), black rot (*Guignardia bidwellii* (Ell.) Viala and Ravaz), root rot, and phylloxera injury. Improved size of berry and better quality would seem desirable. Varieties adapted to the various soil and climatic conditions would be of great assistance to the industry in this region.

In the third region, the northern Great Plains, cold hardiness must of necessity be of primary importance. It would seem possible to combine the cold hardiness of the more northern species with the

Figure 7.—Flower clusters of muscadine grapes. Upper three clusters, staminate blossoms; lower three clusters, pistillate or fruit-bearing blossoms.

size and quality of some of the improved varieties. Some of the more hardy vinifera varieties that mature in a short growing season may be hybridized with the more hardy native species to promote both early maturity and improved quality.

Muscadine Grapes

The muscadine grapes are especially adapted to the Southeastern and Gulf States. Selections have been made from chance seedlings and from the native wild vines of *Vitis rotundifolia*, the muscadine grape. This type of grape is represented commercially by the varieties Eden, James, Mish, Thomas, Scuppernong (fig. 6), and

others less prominent. They are used for table, local markets, juice, and wine. The vines of this type are characterized by vigorous growth, small, nonlobed leaves, simple tendrils, and small fruit clusters, sometimes with only a few berries. The adherence of berry to pedicel is generally poor. The individual berries are globular. The skin is mostly tough and leathery and separates readily from the pulp. The seeds are large and firmly embedded in the pulp. The strong musky flavor is very characteristic.

The present commercial varieties of muscadine grapes are not self-fertile (fig. 7). In commercial plantings it is necessary to include male vines to pollinate the fruiting varieties. Through crosses and selections by the Department at Willard, N. C., a number of self-fertile varieties have been produced. The breeding work at this station has concentrated on the production of these self-fertile, perfect-flowered types. Hybrids have also been obtained between the muscadine grapes and the European and the American bunch-type grapes. The Georgia Experiment Station has also been conducting breeding work with muscadine grapes for improvement in vine and fruit qualities. Eleven muscadine varieties having improved characters have been introduced for commercial trial by the Georgia Station.

Desirable Objectives in Breeding Muscadine Grapes

The muscadine grapes normally have a high resistance to disease and insect injury, and these qualities should be retained. It is desirable to combine quality and size of fruit with the perfect- or hermaphrodite-flowered types. The bunch size might be increased and adherence of the berry to the pedicel developed. The skin might be made more tender and the sweetness and flavor ameliorated by crossing with other grape species. The seeds of the muscadine grapes are larger than those of any other native species, and the development of varieties with smaller seeds would be a decided improvement.

European or Vinifera Grapes

The European or Old World grape types have been developed from the one species, *Vitis vinifera*. The vinifera grape industry in the United States, representing approximately 90 percent of the total commercial grape production, is centered in California, with local plantings in other Western States. The vines of this type are stocky and vigorous to very vigorous in growth. The leaves are medium to very large and usually characteristically lobed. The fruit clusters vary widely with the variety, from very small to very large. The individual berries range from small, as in the seedless currant type, to very large in the table varieties. While the more typical shape of the berries of this type is ovoid, there are globular and elongated forms. The skin adheres to the pulp, whereas the seeds separate readily from the pulp. Some varieties, such as the currant and seedless raisin types, develop without seeds. The fruit is characterized by a relatively high sugar content and a rich vinous flavor. There are types suitable for table use, distant shipping, storage, raisins, juice, and wine (fig. 8). Numerous varieties have been imported from foreign sources for trial in the United States, and of course all of our present commercial vinifera varieties are of foreign origin.

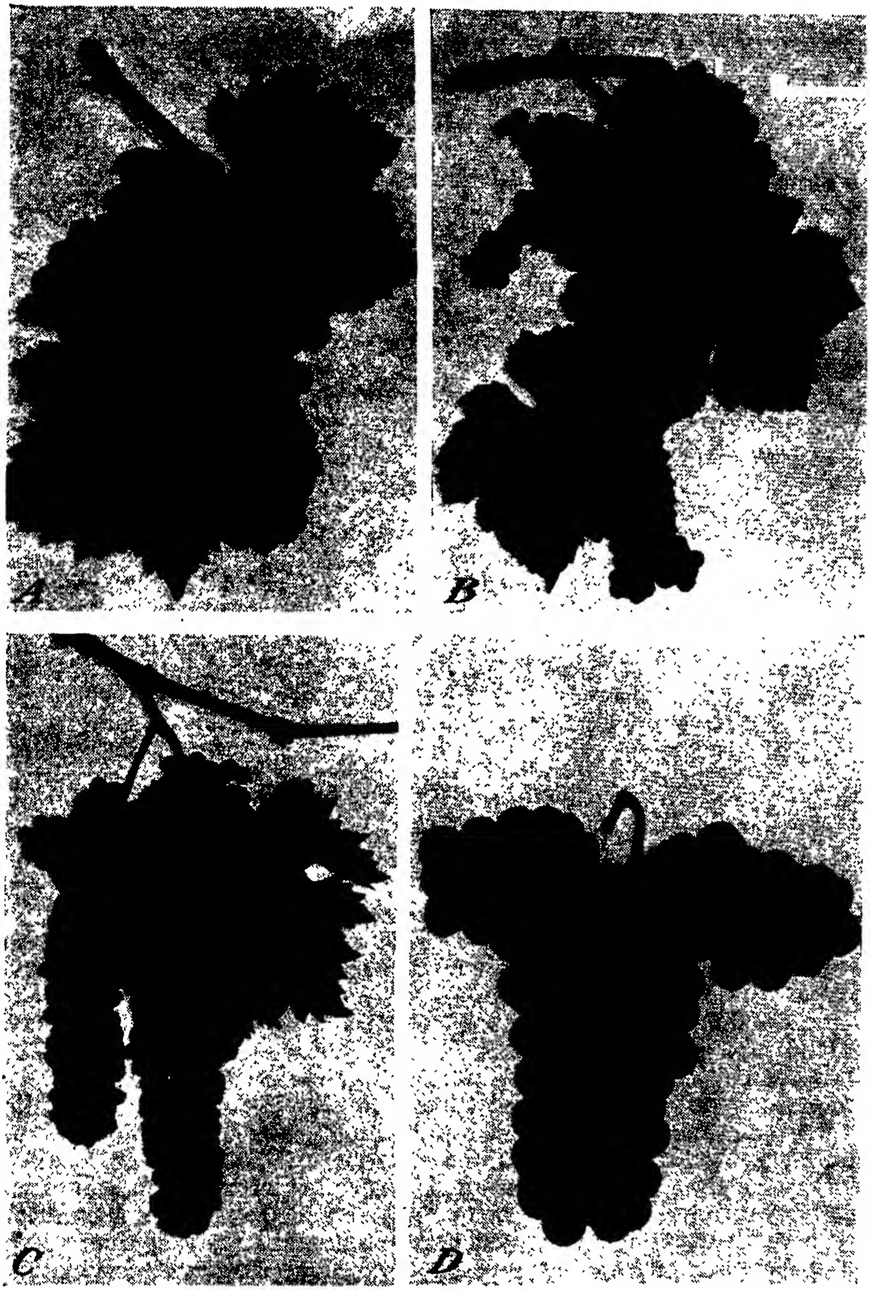

Figure 8.—Typical vinifera grape varieties: *A*, Flame Tokay, table type; *B*, Sultanina (Thompson Seedless), seedless raisin type; *C*, Panariti, currant raisin type; *D*, Petit Syrah, wine type.

The important table varieties are represented by Alexandria (Muscat of Alexandria), Alphonse Lavalle (Ribier), Castiza (Red Malaga), Emperor, Flame Tokay, Malaga, Ohanez, Olivette Blanche, Olivette Noire, and Sultanina (Thompson Seedless). The chief raisin varieties grown are Alexandria, Panariti (Zante currant type), Sultana, and Sultanina. There are many varieties utilized for wine manufacture. The white varieties used for wine include Alexandria, Burger, Chasselas de Fontainebleau, Feher Zagos, Franken Riesling, Gewürz Traminer (pink), Green Hungarian, Muscadelle du Bordelais, Muscat de Frontignan, Palomino, Pedro Ximines, Sauvignon Blanc, Sauvignon Vert, and Semillon. The black varieties include Alicante Bouschet, Aramon, Barbera, Cabernet Sauvignon, Carignane, Cinsaut, Grenache, Mataro, Mission, Mondeuse, Petit Syrah, Refosco, St. Macaire, and Zinfandel.

The trend in vinifera grape breeding in the United States has been to produce more seedless types and improved table, raisin, and wine varieties. Breeding work is being conducted by the Department at Fresno, Calif., and by the California Agricultural Experiment Station at Davis.

At the United States Experiment Vineyard, Fresno, Calif., approximately 500 seedlings have fruited, and seedless-type seedlings have been produced. Earlier maturity has been promoted by crossing early-ripening varieties. Richness of flavor has been transmitted by muscat-flavored varieties. Large-sized berries and a wide range of berry forms have been obtained. Seedlings with red juice adaptable to unfermented juice and to wine manufacture have been produced. Selections have been made of the most promising types for further production tests.

Desirable Objectives in Breeding Vinifera Grapes

In the United States the desirable objectives in breeding vinifera grapes vary with the purpose for which the fruit is intended. The type may be divided into table, raisin, and wine groups, although some varieties may be used interchangeably.

The table group is made up of varieties used locally, shipped to distant markets, and held in cold storage for later use. Since the major portion of the table-grape crop must be shipped from California to the distant eastern markets, firmness of fruit and adherence of berry to pedicel are of primary importance. These qualities are possessed by most of the present shipping varieties. The quality of these table varieties might be improved by the infusion of some of the aroma and flavor of the muscat-flavored grapes. Seedlessness in table grapes has become an important factor. While some seedless varieties are available at present, improvements are possible in size, adherence to stem, quality, color, and extended season of maturity. Improved early- and late-ripening grapes would have a distinct value in prolonging the market season. A storage grape of fine eating quality would be of great value. An assortment of black, red, and white grapes ripening from early to late would supply a demand that is not filled at the present time.

The raisin-grape group at the present time consists of currant-type, seedless-type, and muscat-type varieties. A currant-type

variety with the addition of muscat flavor that would be productive without the annual ringing or cutting of the bark, which is now necessary, would be a decided improvement over present varieties. The present seedless-type raisin varieties could well be increased in size and improved in flavor. A large-sized, seedless, muscat-flavored variety would be very valuable to the raisin industry. A seeded muscat type that would set well-filled, uniform clusters would be a valuable improvement.

In the wine group, many varieties are utilized to make the various kinds of wine. To make certain wine types, the juice of several varieties, often three or more, is blended. It would seem to be within the realm of possibility to blend the varieties by breeding to produce a single variety with all the requirements for a particular kind of wine. Varieties with improved flavors and juice of a more intense and lasting color might be developed. At present all vinifera varieties must be grafted on roots resistant to phylloxera. Some day, varieties resistant to phylloxera, with fruit of desirable quality, may be developed so that grafting will not be necessary. The legalized sale of wines has, of course, furnished an incentive to produce a better product, and this will ultimately result in a greater demand for improved varieties for wine purposes.

EARLY IMPROVEMENT OF GRAPES IN EUROPE

As previously stated, the history of *Vitis vinifera*, the European grape, begins in prehistoric times. During this long period, selection was undoubtedly largely responsible for the numerous varieties concerning the origin of which we have no definite information. Early hybridization work with this species was started by Louis and Henry Bouschet in 1828. Their crosses were made with the definite object of combining the intense color of the Tinto with the high yield of varieties in southern France. Their efforts resulted in the production of three varieties, Alicante Bouschet, Petit Bouschet, and Grand Noir de la Calmette, which are still of commercial importance.

In France, hybridization of native American species assumed very great importance after phylloxera had made the grafting of vinifera varieties on resistant roots necessary. Between 1860 and 1870, diseased spots were noted in many French vineyards. The weakening of the vines was found to be caused by an insect (*Phylloxera vitifoliae* Fitch) living on the roots. Winged forms of the insect, which cause the formation of galls on the leaves, were also found. The phylloxera is indigenous to the eastern and central United States and probably was carried to France before 1860 on rooted American vines imported to resist damage then being caused in Europe by powdery mildew (*Uncinula necator* (Schw.) Burr). Phylloxera spread rapidly over France and the adjacent vine-growing countries. In order to save the vinifera vineyard industry from complete destruction, it was found necessary to graft the European varieties on native American rootstocks, which were resistant to the phylloxera insects. The United States thus furnished both the disease and the cure. Since the American grape species varied in their adaptability to the soil and climatic conditions of Europe, hybrids between American species

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and hybrids between European and native American grapes were utilized for phylloxera-resistant rootstocks.

Some breeding work to combine American and European vines had been started previous to 1876 by the School of Agriculture at Montpellier, France. Foëx, Millardet, Viala, Ravaz, de Grasset, Ganzin, Couderc, Castel, and Seibel practiced similar hybridizing work, which resulted in producing many rootstocks resistant to phylloxera and adapted to different soil types. Direct-producing varieties were also sought that would combine the resistance of the American species with the fruit qualities of *Vitis vinifera*. Many direct-producing varieties were originated through breeding. While the efforts were most successful in producing resistant rootstocks that are used today in the vinifera regions of foreign countries as well as the United States, ideal direct-producing fruit types were not obtained. A start was made, however, which may eventually bring results.

Phylloxera infestations occurred early in the commercial vinifera plantings in California. The only present method of control that has general application is the use of resistant rootstocks on which the vinifera grape varieties are grafted. These rootstocks are of American species and hybrids of American species, though the actual development of them occurred in Europe where phylloxera ravaged the vineyards before it became serious in California. Up to this time, the vinifera grape industry in the United States has depended for stocks on these species selections and hybrids made in Europe. The adaptability of the stocks to the various soil and climatic conditions and their suitability for the vinifera varieties in the United States have been tested by Federal and State workers. Breeding work is now under way for the production of improved stocks for the vinifera regions of the United States.

PRESENT GRAPE-BREEDING WORK IN OTHER COUNTRIES

Czechoslovakia

Investigations in grape breeding in Czechoslovakia are under the direction of Albert Stummer in Nikolsburg and Dr. Franz Frimmel in Brünn. This work, located at the extreme northern edge of commercial grape growing in Europe, includes the testing of resistant stocks, hybridization of varieties to secure wine and table grapes well adapted to northern production, and related investigations. Crossing and selfing of many varieties has been done.

France

French investigators, through selecting and breeding rootstocks resistant to phylloxera and congenial to vinifera varieties, saved the industry of Europe after phylloxera was introduced. A number of privately supported experimental vineyards, as well as a few publicly supported research stations, are still working on resistant understocks. also on hybridizing American species with vinifera varieties to secure varieties sufficiently resistant to grow on their own roots and be resistant to downy mildew (*Plasmopara*) and that will produce fruit of value. Work of this type is under way in the Cognac region.

Germany

Grape breeding is conducted at several points in Germany, as follows:

Alzey Grape Experiment Station (Leader, Grape Inspector Scheu).—Crosses are made with the objective of securing early-ripening and vigorous, good-quality wine grapes and also a series of table-grape varieties ripening from early until extremely late that are well adapted to the Rhineland area. From 15,000 cross-bred seedlings, 450 selections are being tested.

Freiburg; Badisches Weinbauinstitute (Director, Dr. Muller)—Breeding investigations are to secure varieties giving very high wine quality. Crosses of Sylvaner × Rülander have given exceptional wine quality and are being tested on various rootstocks. Resistance of varieties to downy mildew and the development of varieties having dark-red juice are other objectives. Twenty-five selections producing dark-red wine have been made.

Geisenheim a. Rh.; Versuchs- und Forschungsanstalt fur Wein-, Obst- und Gartenbau (Director, Prof. Dr. Rudloff; in charge of grape investigations, Dr. Birk).—The work includes attempts at improvement of the varieties through clone selection; the breeding and testing of phylloxera-resistant rootstocks having good adaptation and an affinity to the important varieties and that are resistant to diseases; and the breeding of early- and late-ripening, high-quality table grapes.

Muncheberg; Kaiser Wilhelm-Institut fur Zuchtungsforschung (Director, Prof. Dr. Rudorf; in charge of grape investigations, Dr. Husfeld and Dr. Scherz).—Investigations are primarily to develop disease-resistant and insect-resistant rootstocks, vines, and varieties. Seedlings are grown by the hundreds of thousands and exposed to disease infection. Fifty thousand seedlings resistant to *Plasmopara* have been found. Their stock compatability and value for wine remain to be tested.

Weinsberg; Wurttembergische Anstalt fur Rebenzuchtung und Rebenpfropfung (Leader, Mr. Herold).—The work consists primarily of the testing of understocks against phylloxera and the development by hybridization and testing of red-wine varieties.

Wurzburg; Staatliche Hauptstelle fur Rebenzüchtung (Leader, Dr. Ziegler).—Breeding investigations include clone selection and hybridization between grape varieties. Some 200 prospective varieties from crosses between varieties are now under test. Breeding of rootstocks resistant to *Plasmopara* and phylloxera, and showing good affinity with varieties, has resulted in about 1,500 selections that appear resistant and are receiving further test. Development of direct producers that combine resistance to phylloxera and diseases with good fruit and wine characteristics is also being attempted.

Italy

Grape-breeding experiments have been actively conducted at various places in Italy. Special attention has been given to the hybridizing of American vines for rootstocks. F. Paulsen, A. Ruggeri, C. Grimaldi, and C. Montoneri, working principally in Sicily, have produced hybrids of American vines for rootstocks. Some of the

more promising productions are Paulsen hybrids (*Vitis berlandieri* × *V. rupestris*) Nos. 771, 775, 779, and 1103; (*V. berlandieri* × (*V. riparia* × *V. rupestris*)) No. 1120; (*V. berlandieri* × (Aramon × Rupestris Ganzin)) No. 1045; (*V. berlandieri* × (Mourvedre × *V. rupestris* 1202)) No. 1323; Ruggeri hybrids (*V. berlandieri* × *V. rupestris* du Lot) No. 140; (*V. berlandieri* × *V. riparia*) Nos. 225, 240, and 325. Other hybrid rootstocks have been originated in Puglia by G. Ceccarelli and V. Prosperi.

Breeding for better table-grape varieties has been conducted by Alberto Pirovano, director of the Institute of Fruit Culture and Electogenetics at Rome. Crosses and backcrosses have been made with a number of vinifera varieties. Amòng the most interesting and noteworthy seedlings produced are Primus, Termidoro, Delizia di Vaprio, Italia, Aurora, Galvani, Perlona, Angelo Pirovano, Teresa Pirovano, and Principessa di Piemonte.

V. Prosperi, director of the Royal Nursery of American Vines at Velletri, has also obtained some interesting table-grape seedlings. Of special note are No. 167 (Moscato de Terracina × Chasselas Vibert) and No. 8 (Panse Precoce × Moscato Fior d'Aranico).

The Royal Experiment Station of Viticulture and Oenology of Conegliano, founded in 1923, began hybridizing work with *Vitis vinifera*. Particular attention has been given to the production of new types of wine and table grapes with regard to their adaptability to the natural conditions of northern Italy. The work of this station was planned by Director G. Dalmasso and L. Manzoni. Italian and French varieties of *V. vinifera* have been used in the grape-breeding work. Better types have been secured so far from crosses of Trebbiano × Traminer, Prosecco × Cabernet Sauvignon, Trebbiano × Verdiso, and Besgano × Moscato de Amburgo. More recently the Conegliano station has started hybridization of *V. vinifera* with American vines, and hybridizing American vines, for the production of new rootstocks more adapted to conditions in the Province of Venezia.

Union of Soviet Socialist Republics

The following outline of the grape investigations in the Union of Soviet Socialist Republics has been taken from Plant Breeding in the Soviet Union, by N. I. Vavilov, published by the Imperial Bureaux of Plant Genetics, Cambridge and Aberystwyth, 1933. Fourteen plant-breeding centers, covering every section of the Soviet Union, constitute regional headquarters for breeding work covering all agricultural crops. These are all under the direction of the Institute of Plant Industry, N. I. Vavilov, director. The grape program includes the following:

(1) Immunity: (*a*) Phylloxera. Breeding resistant varieties by method of cyclic crossing of *Vitis vinifera* with American species and obtaining generations up to F_2 and F_3 (with study of characters of phylloxera). (*b*) Mildew. Breeding resistant varieties by method of cyclic crossing of *V. vinifera* with American species (obtaining generations up to F_2 and F_3, and study of resistance to mildew). (*c*) *Oidium*. Breeding resistant forms by method of cyclic crossing of *V. vinifera* with American species (obtaining generations up to F_2 and F_3, and study of resistance to *Oidium*).

(2) Resistance to frost and cold. Breeding resistant varieties by means of *Vitis vinifera* × *V. amurensis* with study of this character.

(3) Vegetative period. Breeding early and later varieties (in order to extend their cultivation northward) by means of intercrossing of *V. vinifera* and also by crossing with other *Vitis* species.

(4) Chemical characters. Breeding of dessert varieties with transportability, varieties for wine and alcohol-free beverages (sugar and acid content).

(5) Specific characters: (*a*) Preliminary work, on study of characters related to transportability and storing; (*b*) study of seedless varieties in order to obtain productive seedless strains; (*c*) study of character of rooting in *Vitis*.

(6) Problem of sex. Study of heredity of sex in order to obtain self-fertile varieties.

(7) Self-sterility and self-fertility. Study to improve yield.

(8) Permanent modifications. Genetic study (yield of quantitative characters).

(9) The origin of cultivated plants. Comparative genetics of wild *Vitis* species.

(10) Chimeras: (*a*) Study of chimeras in order to find agriculturally valuable characters; (*b*) production of chimeras of practical value; (*c*) qualitative inequality of ontogenetic system of individuals.

Vitis should be included in studies of inbreeding.

Phytopathology and entomology: Methods of inoculation of seedlings with phylloxera, downy mildew, and *Oidium*. Testing of seedlings for resistance to phylloxera under various ecological conditions.

Physiology Stimulation of seedlings and seeds to accelerated growth and fruit bearing.

Australia

The Department of Agriculture, New South Wales, Australia, at its Yanco Experiment Farm, started grape breeding in 1928, under the direction of H. Wenholz, to produce a black table grape of high quality and with the shipping quality of Ohanez. Breeding for disease resistance and for the production of seedless raisin and table varieties has been in progress.

ACHIEVEMENTS AND NEEDS

The major portion of the grape-breeding work has been to improve quality. Quality is an elusive factor. In quality of fruit, native American types are considered inferior to the vinifera types. The quality of fruit has been improved where our native varieties have been crossed with the best-quality varieties of *Vitis vinifera*. Improvements in cluster and berry types have been made by combining different native species. Grape rootstocks have been developed through hybridization which have suitable resistance to phylloxera and are adapted to various soil types.

The results so far obtained indicate that grape improvements can be obtained through hybridization. The field of grape breeding is still relatively new. There is need for more information, especially on the inheritance of desirable characters such as size, quality, seedlessness, cold hardiness, disease and insect resistance, and adaptability to environment. Collections of species, native American varieties, and European varieties are available as breeding material. Progress has been made, but continued improvement is possible. Better quality, more attractive appearance, and a prolonged season will result in increased demand and consumption, to the ultimate profit of the grape industry.

INHERITANCE IN GRAPES [3]

Early grape breeding was carried on mainly to obtain desirable varieties or stocks, and little attention was given to the study of inherita-

[3] The following pages are written primarily for students and others professionally interested in breeding or genetics

ble qualities. As intensive breeding work has been in progress a relatively short time, and the time necessary from seed to fruit in one generation of grapes occupies ordinarily from 3½ to 5½ years, only limited data are available on the transmission of inheritable qualities. Genetic and cytological research projects at State and Federal institutions are listed in the appendix material.

The somatic chromosome number of most vinifera grapes and most American bunch-grape species is 38. Gigas forms of American and vinifera varieties are tetraploids with 76 chromosomes in the somatic tissues. Most American bunch-grape species will cross readily with one another and with vinifera varieties, forming fully fertile hybrids. The two muscadine species cross freely with each other, with fertile hybrids resulting. The muscadines and vinifera varieties or American bunch-grape types are crossed with some difficulty, and the F_1 hybrids of these crosses generally set but few if any fruits.

One important commercial consideration concerns the character of grape flowers—whether the stamens are upright or reflex. At the New York (State) Agricultural Experiment Station, crossing two varieties with reflex stamens gave in the F_1 a ratio of 1 reflex to 1 upright in the resultant progeny. Crossing upright stamens with reflex stamens gave the same ratio, while crossing two varieties with upright stamens gave 4.3 upright to 1 reflex in the F_1 progeny. From crosses of vinifera varieties with upright stamens at the United States Experiment Vineyard, Fresno, Calif., the ratio of upright to reflex stamens in the F_1 seedlings was 5.4 to 1.

In color of fruit, white is a recessive character, and only white-fruited progeny results when two white-fruited varieties are crossed. Both red and black are dominant over white, and most of the red and black varieties studied appear to be heterozygous for color.

The investigations of Hedrick and Anthony (*5*) at Geneva, N. Y., reported in 1915, relative to color, indicated that crosses of black-fruited and white-fruited varieties gave in the F_1 approximately 3 black-fruited seedlings to 1 white-fruited. Black-fruited and red-fruited varieties segregated into these colors only when selfed or crossed. At the United States Experiment Vineyard at Fresno, Calif., the segregation obtained in the first and later generations of crosses among varieties with colored fruit has varied with the different parent varieties used. It would appear that the majority of colored grapes on which data are available are heterozygous for both red and black color.

During recent years attention has been given to the origination of more seedless varieties of grapes through breeding. A. B. Stout, of the New York Botanical Garden, in cooperation with the New York (State) Agricultural Experiment Station, has produced seedless or near-seedless types by using the pollen from the present seedless vinifera varieties to pollinate American-type varieties. At the United States Experiment Vineyard, Fresno, Calif., crosses have been made between the seedless vinifera varieties and many of the seed-bearing vinifera varieties. Of the seedlings that have fruited to date, 12.4 percent have produced seedless-type fruit in the F_1 generation. The production of seedlessness in the F_1 generation has proved the value of seedless varieties as male parents to produce new seedless types.

While the inheritable factor for seedlessness has not been determined, progress has been made in developing more seedless varieties for breeding work, some of which may also be of commercial value.

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APPENDIX

LOCATION OF PRESENT GRAPE BREEDING IN THE UNITED STATES AND INVESTIGATORS CONDUCTING THE WORK

United States Department of Agriculture, Bureau of Plant Industry, Division of Fruit and Vegetable Crops and Diseases:
- Beltsville, Md.: C. A. Magoon, I. W. Dix, J. R. Magness.
- Fresno, Calif.: Elmer Snyder, F. N. Harmon.
- Meridian, Miss.: N. A. Loomis.
- Willard, N. C.: C. T. Dearing.

State agricultural experiment stations:
- California, Davis: H. P. Olmo.
- Georgia, Experiment: H. P. Stuckey.
- Maryland, College Park: A. L. Schrader, S. W. Wentworth.
- Minnesota, University Farm, St. Paul: A. N. Wilcox.
- Missouri, Mountain Grove: Paul H. Shepard.
- New York:
  - Geneva: Richard Wellington and coworkers.
  - Fredonia: F. E. Gladwin.
  - New York Botanical Garden, Fordham Station, New York: A. B. Stout.
- South Dakota, Brookings: N. E. Hansen.
- Texas, College Station: S. H. Yarnell.
- Virginia, Blacksburg: F. W. HofMann.

Summary of Present Grape Breeding in the United States

California

Main grape breeding work started in 1931 to produce new seedless varieties, improve the quality of table varieties, and to study genetic factors. Crosses and selfed varieties have yielded approximately 3,000 seedlings. The chromosome number for Sultanina was found to be 38 and of the Gigas types to be 76. Breeding material includes a large number of vinifera varieties and a collection of native American species. Selfed seedlings are being grown of the following varieties: Alexandria (Muscat of Alexandria), Alphonse Lavallee (Ribier[4]), Angulato, Black Corinth, Chaouch, Chasselas Cioutat, Diamond Jubilee, Emperor, Flame Tokay, Gros Colman, Hunisa × Muscat, Malaga, Malvasia Bianca, Molinera, Muscatello Fino, and Ohanez.

Seedlings have been obtained from the following crosses: Alexandria × Black Corinth, Alexandria × Sultana, Alexandria × Sultanina, Alexandria × Sultanina Gigas, Alexandria × Sultanina Rosea, Alexandria × White Corinth, Alphonse Lavallee × Monukka, Alphonse Lavallee × Sultana, Alphonse Lavallee × Sultanina, Alphonse Lavallee × Sultanina Gigas, Augibi × Sultanina, Black Morocco × Golden Muscat, Burgrave × Monukka, Burgrave × Sultanina, Chaouch × Alexandria, Chaouch × Black Corinth, Chaouch × Monukka, Chaouch × Sultana, Chaouch × Sultanina, Damas Rose × Monukka, Damas Rose × Sultanina, Damas Rose × Sultanina Gigas, Dattier de Beyrouth × Monukka, Dattier de Beyrouth × Sultanina, Diamond Jubilee × Monukka, Diamond Jubilee × Sultanina, Emperor × Monukka, Emperor × Sultanina, Flame Tokay × Black Corinth, Flame Tokay × Monukka, Flame Tokay × Sultana, Flame Tokay × Sultanina, Flame Tokay × Sultanina Rosea, Flame Tokay × White Corinth, Golden Muscat × (Hunisa × Muscat), Golden Muscat × Sultanina, Gros Colman × Monukka, Gros Colman × Sultanina, Gros Colman × Sultanina Gigas, Gros Colman × Sultanina Rosea, Henab × Monukka, Hunisa × Black Corinth, Hunisa × Golden Muscat, Hunisa × Monukka, Hunisa × Sultanina, Hunisa × Sultanina Gigas, (Hunisa × Muscat) × Golden Muscat, (Hunisa × Muscat) × Malvasia Bianca, (Hunisa × Muscat) × Alexandria, Madeleine Angevine × Luglienga, Madresfield Court × Monukka, Madresfield Court × Sultanina, Malvasia Bianca × Sultanina, Marvel de Vaucluse × Malvasia Bianca, Molinera × Monukka, Molinera × Sultanina, Muscat Blowers × Monukka, Muscat Blowers × Sultanina, Muscat Bowood × Black Corinth, Muscatello Fino × Sultanina, Muscat Gigas × Alexandria, Muscat Hamburg × Sultanina, Olivette Blanche × Monukka, Olivette Blanche × Sultanina, Rambela × Monukka, Rambela × Sultanina, Trivoti × Monukka, Trivoti × Sultanina, Zabalkanski × Monukka.

Georgia

Grape-breeding work is entirely with *Vitis rotundifolia* to improve vine and fruit qualities of the muscadine grapes. Eleven varieties have been introduced from 1919 to 1934. Breeding material includes a number of muscadine varieties and station seedlings. Table 3 gives the varieties introduced.

Table 3.—*Grape varieties introduced by the Georgia Experiment Station*

Variety	Year introduced	Parentage	Qualities
Brownie	1933	San Monta × white male	Productive; high sugar content.
Dulcet	1934	Hunt × white male	
Howard	1921	Scuppernong × black male	High sugar content.
Hunt	1919	Flowers × white male	Productive; adherence; thin skin.
Irene	1919	Thomas × black male	Vigorous; adherence; large.
Lucida	1933	Irene × unknown male	Large; attractive appearance.
November	1919	Scuppernong × black male	Productive; good clusters; late.
Qualitas	1919	Thomas × black male	Good quality; sweet.
Spalding	1919	Flowers × white male	Good clusters; long season.
Stuckey	1919	Scuppernong × black male	Large; white; sweet.
Yuga	1934	San Monta × unknown male	Attractive; compact; thin skin.

[4] Alphonse Lavallee is grown commercially in California under the name Ribier.

Maryland

Grape-breeding work was started in 1912. The main attempts were to develop an early black grape of high quality. A study was made of the inheritance of fruit color. While an early black grape of quality for Maryland conditions was not obtained, a few seedlings were propagated in 1929 for further test, some of which show promise as desirable varieties.

Seedlings were grown of the following open-pollinated varieties: Bailey, Brilliant, Creveling, Goethe, Lindley, Lucile, Mericadel, Red Giant, Salem, Wilder, Woodruff, Worden, Wyoming. Seedlings were also obtained from the following crosses: Agawam × Clinton, Brighton × Winchell, Campbell × Winchell, Clinton × Black Hamburg, Delicious × Winchell, Diana × Clinton, Diamond × Clinton, Eclipse × Brilliant, Lindley × Clinton, Lindley × Campbell Early, Lindley × Winchell, Moore Early × Winchell, Salem × Clinton, Winchell × Brilliant, Winchell × Clinton, Winchell × Worden, Worden × Winchell, Worden × Clinton.

Minnesota

Grape breeding has been in progress since 1908. The early work stressed the use of Beta as a hardy parent in combination with the higher quality varieties, Agawam, Campbell, Concord, Delaware, Janesville, Jessica, Lutie, Salem, and Witt. In later work since 1923, selected seedlings from these crosses have been used in further breeding work by intercrossing, crossing with various dessert varieties, and inbreeding. Breeding studies have been conducted, principally with respect to winter hardiness. Selections have been made to develop homozygous material for genetic studies and for superior value in breeding work. Cytological studies have been made on pollen development with special reference to sterility. A chromosome number of 38 was determined in the Beta grape, using root-tip material in making the count determinations.

Missouri

Grape breeding has been in progress since 1933. Earlier crosses were made with the objective of better quality, improved vigor, and more resistance to disease. Seedlings have been obtained from the following grape crosses: Campbell Early × Eaton, Columbia × 42–18, Concord × Caco, Concord × Eaton, Concord × 42–18, Concord × Triumph, 42-2 × 42-8, 44–5 × Caco, 44–5 × Concord, Goethe × Concord, Goethe × 42–8, Herbert × Agawam, Herbert × Concord, Herbert × 42–8, Hubbard × Beta, Eclipse × Eaton, Eclipse × 42-8, Eclipse × Triumph, Lindley × Caco, Lindley × Concord, Lindley × 42-8, Lindley × 42–17, Lindley × Triumph, Moore Early × Caco, Moore Early × Concord, Muench × Beta, Muench × 42–17, Muench × Triumph, Triumph × Concord, Triumph × Eaton, Triumph × 42–17, Triumph × Portland.

In 1935 Concord and Moore Early were crossed with Lindley, Herbert, and Barry (Rogers hybrids) to develop self-fertile varieties with some of the desirable qualities of the Rogers hybrids.

New York

Grape-breeding work at Geneva was started in 1888. More than 30,000 grape seedlings have been grown at this station. Selfing and crossing have been used extensively. Of 282 selfed varieties and selfed seedlings, no seedling appeared worthy of commercial trial. Three hundred and twenty-five varieties and seedlings have been used in the breeding work. Particular attention has been given to vigor, hardiness, productiveness, disease resistance, and quality of fruit. In connection with the breeding work, a study has been made of the transmission of different characters. Reports have been made on the inheritance of stamen characters, color of fruit, and transmission of other vine and fruit qualities. Chromosome counts give a diploid number of 38 in the grape varieties and species studied, excepting several Gigas strains, which give a count of 76. Some seedlings with the triploid chromosome number have recently been produced.

In cooperation with the New York Botanical Garden, extensive breeding work has been carried on mainly for the production of seedless varieties suitable to eastern conditions. Reports have been issued covering this phase of the work. From 1907 to 1937, 21 varieties have been introduced as the result of breeding work conducted at Geneva and Fredonia, N. Y., and in cooperation with the New York Botanical Garden (table 4).

Table 4.—*Grape varieties introduced by the New York State Agricultural Experiment Station (Geneva and Fredonia)*

Variety	Year introduced	Parentage	Superior characters
Brocton	1919	Brighton × (Winchell × Diamond)	Productive: white; oval.
Bronx Seedless	1936	(Goff × Dina) × Sultanina	Productive; red.
Dunkirk	1920	Brighton × Jefferson	Medium productive; red.
Fredonia	1915	Champion × Lucile	Large cluster and berry.
Goff	1907	Goff seedling no. 19	Productive; reddish black.
Golden Muscat	1927	Muscat Hamburg × Diamond	Very productive; large cluster; white.
Hanover	1928	Brighton × Niagara	Productive: red.
Keuka	1923	Chasselas Rose × Mills	Productive; red; late.
Melton	1923	Triumph × ((Winchell × Diamond) × Jefferson).	Productive; white.
Ontario	1908	Winchell × Diamond	Productive; white; early.
Pontiac	1922	Herbert × Worden	Medium productive; black.
Portland	1912	Champion × Lutie	Productive; early; white.
Ripley	1912	Winchell × Diamond	Productive; white.
Seneca	1930	Lignan Blanc × Ontario	Medium productive; early; white.
Sheridan	1921	Herbert × Worden	Productive; black.
Stout Seedless	1930	(Triumph × Dutchess) × Sultanina Rosea.	Medium productive; white.
Urbana	1912	Ross × Mills	Medium productive; red; late.
Van Buren	1924	Fredonia × Worden	Earliness.
Watkins	1930	Mills × Ontario	Medium productive; nearly black.
Wayne	1927	Mills × Ontario	Productive; black.
Westfield	1922	Herbert × Concord Seedless	High sugar; high color.

From the following crosses at the New York (Geneva) station, 6 seedlings have been propagated for naming, 35 for extensive trial, and 69 for a small trial: Ontario × Sheridan, Sheridan × Ontario, Ontario × Gros Guillaume, Ontario × Black Corinth, Ontario × Hubbard, Ontario × Moore Early, Ontario × Muscat Hamburg, Eclipse × Portland, Iona × Ontario, Herbert × Watkins, Concord × Sta.[5] 10085 (Triumph × Mills), Sta. 10115 (Triumph × Mills) × Concord, Portland × Moore Early, Wayne × Iona, Hubbard × Gros Guillaume, Hubbard × Golden Muscat, Zinfandel × Ontario, Mead No. 9 × Noir Hatif de Marseille, Golden Muscat × Wayne, Golden Muscat × Sultanina, Sta. 10842 ((Herbert × Triumph) × (116 × Jefferson)) × Sultana, Sta. 7408 (Ross × Mills) × Moore Early, Sta. 8691 ((Iona × Vergennes) × Jefferson) × Khalili, Sta. 8691 (Iona × Vergennes) × Muscat Hamburg, Sta. 8717 (Kensington × Triumph) × Watkins, Sta. 9104 (Triumph × Iona) × Seneca, Sta. 9104 (Triumph × Iona) × Seneca, Sta. 10420 (Muscat Hamburg × Ripley) × Khalili, Sta. 10439 (Bakator × Diamond) × Seneca, Sta. 10526 (Muscat Hamburg × Ripley) × Melton, Sta. 10774 (Chasselas Besson × Diana) × ((Triumph × Sta. 116) × Jefferson) × Muscat Hamburg, Sta. 10605 (Frankenthal Precoce × Diamond) × Ontario, Sta. 10108 (Triumph × Mills) × Ontario, Sta. 10144 (Mills × Triumph) × Dunkirk, Sta. 8536 (Goff × Iona) × Ontario, Sta. 7408 (Ross × Mills) × Ontario, Sta. 10526 (Muscat Hamburg × Ripley) × Khalili. Principal grape varieties used in breeding work by the New York (State) Station:[6] Agawam, Barry, Berckmans, Brighton, Butler, Campbell, Catawba, Champion, *Chasselas Golden, Chasselas Rose, Clinton, Colerain, Collier, Concord, Concord Seedless, Cottage, Croton, Daisy, Delaware, Diamond, Diana, Dutchess, Eclipse, Franken Riesling, Fredonia, Goethe, Golden Muscat, *Herbert, Hubbard, Hubbard Seedless, *Iona, Jessica, Keuka, Lindley, Lucile, Manito, Massasoit, Melton, *Mills, Moore Early, *Muscat Hamburg, Noah, *Ontario, Panariti, Pekin, Petit Syrah, Portland, Regal, Ripley, Rosaki, Salem, Secretary, Seneca, Sheridan, Stout Seedless, Triumph, Urbana, Vergennes, Wayne, Winchell, Worden, and also station seedlings nos. 7408, 8536, 9130, and 10919.

Grape material available for breeding in addition to American Euvitis varieties includes early-maturing vinifera varieties and the following list of unusual varieties:

From Africa: Primativo, Roussanne.

French hybrids: Caperan, Commandant, Bertile, Seyve 2667, Cartier 1, Malegue 2049–3, Peage 5–10, Seibel 2, 14, 1000, 4629, 4643, 5136, 5296, 5437, 5455, 5760, 5898, 6339, 6905, Villard 2–108.

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[5] "Sta." denotes station seedling.

[6] An asterisk (*) denotes varieties that have made good parents; others may appear later.

From Hungary: Königin Elizabeth, Königin der Weingarten, Malaga Bleu, Millenium Straube, Szauter Musk.

From Union of Soviet Socialist Republics: Albourla, Aneb-el-Cadi, Apapnish White, Buaki, Charas, Hisakasy, Maska, Muscat de Crime, Rish Baba, Rosy Taifi, Sabsa, Said Galumi, Shuvargani, Tabyrn, Ter-Gulmer, White Chilaki.

South Dakota

Many seedlings of the wild grape of the Dakotas were grown, but little variation and no apparent improvement over the wild type was noticed. This led to the crossing of the wild grape of the Dakotas with choice American-type grapes. The hardiness of the wild type, *Vitis vulpina*, appeared to be strongly dominant, and 32 varieties that appeared hardy and that have superior fruit qualities for the more northern regions were introduced in 1925.

Table 5 indicates the parentage and some of the superior qualities of grape varieties introduced by the South Dakota Station.

Table 5.—*Grape varieties introduced by the South Dakota Agricultural Experiment Station*

Variety	Parentage	Qualities
Arikara	Lady × North Dakota wild	White; productive, large
Atkan	do	White, sweet, long bunch.
Azita	Beta × North Dakota wild	Sweet; vigorous, medium size
Caddo	Beta × Agawam	Black; sweet, good flavor
Chonkee	Lady × North Dakota wild	White; productive, vigorous
Chontay	Massasoit × Beta	Black; vigorous; good flavor
Edapa	Merrimac × Beta	Black; large; good quality
Emana	Beta × Agawam	Black, large, good flavor
Eona	Lady Washington × Beta	White; productive; sweet
Lachala	Lady × North Dakota wild	White; productive, large
Luza	Merrimac × Beta	Red, sweet; meaty
Mandan	Wilder × North Dakota wild	Black, productive, early
Manota	Merrimac × Beta	Black; large; good quality
Napka	Salem × Beta	Black; vigorous, good flavor
Nompah	Lindley × South Dakota wild	Black, large, good flavor
Oglala	Merrimac × Beta	Black, productive; large
Onaka	Beta × Salem	White, productive, large
Osbu	Beta × Agawam	Black, medium size, good flavor.
Pontigo	Lady × North Dakota wild	Light red, very large sweet
Ree	do	White, productive late
Santee	Merrimac × Beta	Black, productive, large
Shakoka	Lady × North Dakota wild	Black, vigorous, large
Siposka	do	Black, large.
Sonona	do	Light red, productive, sweet
Tahama	do	Black; vigorous, large
Teopa	Lindley × South Dakota wild	White, sweet
Toscha	Lady × North Dakota wild	White, sweet, large.
Wachepa	Lady Washington × Beta	Do.
Wakpala	Merrimac × Beta	Black; very large, good flavor
Wecota	Lady Washington × Beta	White, sweet
Wetonka	Beta × Salem	Black, productive, vigorous
Yasota	Merrimac × Beta	Black, large, wild flavor

Texas

Grape-breeding work started in 1935. Seedlings of selfed and crossed varieties are being obtained in an attempt to improve fruiting varieties relative to vigor, adaptability, disease resistance, and fruit qualities. Breeding material includes vinifera and native varieties and native grape species. Seedlings have been obtained from the following selfed varieties: Allaga, Elvicand, Extra, Lomanto, Marguerite, Mathilda, and R. W. Munson.

Virginia

Grape-breeding work started in 1930 by raising seedlings of open-pollinated standard varieties. Varietal crosses of American native varieties were made in 1935. The main objective is to improve the flesh quality. A study is being made of pollen compatibility, fruit characters, and resistance to disease.

From open-pollinated blossoms seedlings have been grown from the following varieties: Catawba, Concord, Eumelan, Moore Early, Niagara, and Worden.

Seedlings are also being grown from the following controlled crosses: Agawam × Amber Queen, Agawam × Barry, Agawam × V. L. B., Amber Queen × Agawam,

Amber Queen × Catawba, Eumelan × Catawba, Eumelan × Delaware, Eumelan × Wilder, Eumelan × Worden, Eumelan × V. L. B., Niagara × Worden, Wilder × Amber Queen, and selfed seedlings of Agawam, Catawba, Delaware, and Regal.

Two seedlings of earlier crosses were introduced in 1936: V. L. B. (Campbell Early × Herbert) and Agel (Agawam × Regal).

United States Department of Agriculture

Grape-breeding work was started with vinifera varieties at Fresno, Calif., in 1923, to produce seedless varieties suitable for table and raisin use, quality table varieties, and juice varieties Crosses have been made between many vinifera varieties, using the seedless varieties as the male parents. Large-berry varieties have been used to increase size, and highly flavored varieties to improve quality. Seedlings of standard varieties, selfed seedlings, and backcrosses are being grown to study genetic characters and the possibility of obtaining desirable qualities. Some cytological work has been done on pollen development and the development of the ovule. Studies have been made on the inheritance of vine, flower, and fruit characters.

Seedlings are being grown of phylloxera-resistant stock varieties and crosses of stock varieties for further studies on rootstocks resistant to root knot nematode. Varietal improvement through the selection of bud sports is in progress. Publications have been issued on the progress of the breeding work and the production of seedless varieties. Grape-breeding material includes 338 American native varieties, 95 Franco-American direct producers, 136 phylloxera-resistant rootstocks, over 550 varieties of *Vitis vinifera*, and in addition over 200 more recent Plant Introduction numbers from foreign sources.

Seedlings of the following crosses have been obtained: Alexandria × Alicante Bouschet, Alexandria × Monukka, Alexandria × Calmette, Alexandria × Corinthe Blanc, Alexandria × Corinthe Rose, Alexandria × Damas Rose, Alexandria × Hunisa, Alexandria × Malaga, Alexandria × Panariti, Alexandria × Sultanina, Alexandria × Sultanina Gigas, Alexandria × Sultanina Rosea, Emperor × Monukka, Emperor × Maraville de Malaga, Emperor × Sultanina, Flame Tokay × Monukka, Flame Tokay × Maraville de Malaga, Flame Tokay × Sultanina, Gros Guillaume × Monukka, Gros Guillaume × Maskah, Gros Guillaume × Sultanina Gigas, Malaga × Monukka, Malaga × Sultanina, Maraville de Malaga × Monukka, Maraville de Malaga × Sultanina, Maraville de Malaga × Sultanina Gigas, Maraville de Malaga × Tagonti Rouge, Maskah × Gros Guillaume, Muscat Hamburg × Monukka, Muscat Hamburg × Panariti, Ohanez × Monukka, Panariti (sport) × Monukka, Pizzutella × Monukka, Rodites × Monukka, Rodites × Gros Guillaume, Vigne de Zericho × Rodites.

Seedlings have been obtained from crosses of station seedlings and standard varieties as follows: (Alexandria × Monukka) 9642 × Monukka, (Alexandria × Monukka) 96419 × Monukka, (Alexandria × Corinthe Rose) 105616 × Monukka, (Alexandria × Corinthe Rose) 105713 × Monukka, (Alexandria × Sultanina) 96212 × Sultanina, (Damas Rose × Monukka) 8635 × Monukka, (Damas Rose × Monukka) 86310 × Monukka, (Damas Rose × Monukka) 8649 × Sultanina Gigas, (Damas Rose × Monukka) 86311 × Sultanina Gigas, (Muscat Hamburg × Monukka) 106212 × Monukka, (Muscat Hamburg × Monukka) 106312 × Monukka, (Pizzutella × Monukka) 10644 × Monukka, (Pizzutella × Monukka) 10649 × Monukka, and Muscat Hamburg × (Alexandria × Sultanina Rosea) 96212.

Seedlings of the following selfed varieties are being grown: Agadia, Alexandria, Carignane, Chasselas Cioutat, Chasselas Doré, Chasselas Rose de Falloux, Cinsaut, Crabbs Burgundy, Emperor, Flame Tokay, Foster, Gros Guillaume, Lenoir, Malaga, Maraville de Malaga, Maskah, Mission, Muscat Hamburg, Mondeuse, Panariti, Palomino, Petit Syrah, Prune de Cazouls, Sauvignon Vert, Semillon, Sylvaner, Traminer, Zeinc, Zinfandel, and seedlings of the following Plant Introduction nos. 105074 to 107086, inclusive, 105922, and 107007.

Seedlings of the following selfed station seedlings are being grown: (Alexandria × Alicante Bouschet) 9582, (Alexandria × Alicante Bouschet) 95915, (Alexandria × Alicante Bouschet) 95919, (Alexandria × Monukka) 9623, (Alexandria × Monukka) 9627, (Alexandria × Monukka) 9628, (Alexandria × Monukka) 96311, (Alexandria × Monukka) 96317, (Alexandria × Monukka) 96319, (Alexandria × Monukka) 9642, (Alexandria × Monukka) 9646, (Alexandria × Monukka) 96419, (Alexandria × Calmette) 96017, (Alexandria × Corinthe Rose) 105616, (Alexandria × Malaga) 9571, (Alexandria × Malaga)

95818, (Alexandria × Malaga) 10587, (Alexandria × Malaga) 105915, (Alexandria × Panariti) 9603, (Alexandria × Panariti) 9118, (Alexandria × Sultanina) 96212, (Alexandria × Sultanina Rosea) 9612, (Alexandria × Sultanina Rosea) 96216, (Muscat Hamburg × Monukka) 106211, (Muscat Hamburg × Monukka) 106212, (Muscat Hamburg × Monukka) 10633, (Muscat Hamburg × Monukka) 10637, (Muscat Hamburg × Monukka) 106312, (Muscat Hamburg × Monukka) 106316, (Muscat Hamburg × Panariti) 8621, (Muscat Hamburg × Panariti) 8623, (Olivette Blanche × Muscat Hamburg) 10616, (Olivette Blanche × Muscat Hamburg) 10626, (Olivette Blanche × Olivette Noire) 9563, (Olivette Blanche × Olivette Noire) 9564, (Olivette Blanche × Olivette Noire) 9566, (Olivette Blanche × Olivette Noire) 9572, (Pizzutella × Monukka) 10649.

Seedlings of Vinifera grape crosses that have fruited at the Fresno station of the United States Department of Agriculture

Parentage	Superior qualities obtained
Alexandria × Alicante Bouschet	Productive; vigorous; red juice; rich flavor.
Alexandria × Monukka	Productive; vigorous; seedless; muscat flavor; adherence.
Alexandria × Calmette	Productive; red juice; rich flavor.
Alexandria × White Corinth	Productive; all white fruit.
Alexandria × Corinthe Rose	Productive; some red fruit; rich flavor.
Alexandria × Damas Rose	Productive; large-size berry.
Alexandria × Hunisa	Vigorous.
Alexandria × Malaga	Productive; large-size cluster and berry; rich flavor.
Alexandria × Panariti	Productive; none seedless.
Alexandria × Sultanina	Productive; vigorous; seedless; no muscat flavor.
Alexandria × Sultanina Rosea	Productive; vigorous.
Damas Rose × Monukka	Productive; vigorous; large size; some seedless.
Gros Guillaume × Monukka	Adherence; large size; seedless.
Muscat Hamburg × Monukka	Productive; muscat flavor; some seedless.
Muscat Hamburg × Panariti	Productive; small size; none seedless.
Ohanez × Monukka	Seedless; late ripening.
Olivette Blanche × Muscat Hamburg	Elongated types; muscat flavor.
Olivette Blanche × Olivette Noire	Elongated types; white, red, and black colored fruit.
Pizzutella × Monukka	Elongated fruit types; seedless; early ripening.
Rodites × Monukka	Late ripening; seedless.
Rodites × Gros Guillaume	Late ripening; firmness of fruit.

Grape-breeding work with native American grapes and *Vitis vinifera* has been in progress at Arlington, Va., and Beltsville, Md., since 1933, to originate seedless varieties and to improve the quality and adaptability of native American varieties especially for central and southern regions.

Seedlings of the following varieties are under observation at the Beltsville station: August Giant, Bailey, Black Eagle, Caco, Captain, Captivator, Ellen Scott, Eumelan, Golden Muscat, Goff, Manito, Mills, Nitodal, Norwood, Oriental, Rogers nos. 13, 32, 33, Urbana.

Seedlings have been obtained of the following native bunch grape crosses: Bailey × Brilliant Seedling, Captivator × Beacon, Captivator × Columbian Imperial, Captivator × Fredonia, Champanel × Manito, Champanel × Niagara, Columbian Imperial × Empire State, Delaware × Goethe, Empire State × Manito, Goethe × Delaware, Lenoir × Salem, Loretto × Oriental, Manito × Caco, Manito × Empire State, Oriental × Portland, Rogers 13 × Beta.

Seedlings have been obtained of the following native American bunch grapes and vinifera crosses: Atoka × Gros Guillaume, Bailey × Foster, Bailey × Goolabie, Bailey × Gros Guillaume, Blauer Portugieser × Monukka, Campbell Early × Monukka, Campbell Early × Alphonse Lavallee (Ribier [7]), Captain × Goolabie, Captivator × Monukka, Captivator × Alphonse Lavallee, Catawba × Monukka, Catawba × Muscat Hamburg, Catawba × Alphonse Lavallee, Catawba × Sultanina, Cloeta × Goolabie, Cloeta × Muscat Hamburg, Columbian Imperial × Monukka, Columbian Imperial × Goolabie, Concord × Monuk-

[7] See footnote 4, p. 656.

ka, Concord × Sultanina, Ellen Scott × Sultanina, Lucile × Monukka, Manito × Chasselas de Fontainebeau, Manito × Alphonse Lavallee, Niagara × Sultanina, Ontario × Blauer Portugieser, Oriental × Albardiens, Oriental × Monukka, Oriental × Goolabie, Oriental × Muscat Hamburg, Oriental × Panariti Oriental × Sultanina, Portland × Blauer Portugieser, Triumph × Monukka, Vergennes × Monukka, Vergennes × Alphonse Lavallee.

Muscadine grape-breeding work of the Department has been centered at the North Carolina State Department of Agriculture Test Farm, Willard, N. C. This work was started in 1907. From two early crosses, two perfect-flowered hermaphrodite seedlings were obtained. By selfing one of these plants, and also by using the pollen from this type to pollinate standard muscadine varieties, an additional number of perfect-flowered seedlings were obtained. Better berry adherence, increased productivity, and improved fruit quality have been reported. True hybrids were obtained between *Vitis rotundifolia* and *V. vinifera*, and also between *V. rotundifolia* and varieties of American bunch-type grapes.

The following hybrid seedlings of *Vitis rotundifolia* and varieties of American bunch-type grapes obtained at Willard, have been selected for further study: James × Winchell, Labama × Brilliant, muscadine seedling × Campbell Early, muscadine seedling × Catawba, muscadine seedling × Delaware, muscadine seedling × Goethe, muscadine seedling × Winchell, Scuppernong × Louisiana, San Jacinto × Ives, Thomas × Concord, Thomas × Goethe.

The following hybrid seedlings of *Vitis rotundifolia* and *V. vinifera* have been selected for further study: George × Goolabie, muscadine seedling × Black Morocco, muscadine seedling × Semillon, San Alba × Malaga, San Alba × Semillon, San Jacinto × Malaga, Thomas × Black Morocco, Thomas × Maraville de Malaga.

Muscadine seedlings selected for further trial are the following: 10- Latham × (Eden × (Eden × male Munsoniana)), 14- Latham × (Thomas × (Eden × (Eden × male Munsoniana))), 3- Latham × male (muscadine seedling × (Eden × (Eden × male Munsoniana))), 1- Latham × male (muscadine seedling × (Eden × male Munsoniana)), 8- Luola × (Eden × (Eden × (Eden × male Munsoniana))), 3- Luola × (Thomas × (Eden × (Eden × male Munsoniana))), 5- Luola × (muscadine seedling × (Eden × (Eden × male Munsoniana))), 1- Luola × (muscadine seedling × (Eden × (Eden × male Munsoniana))), 1- San Alba × (Eden × (Eden × male Munsoniana)), 2- San Alba × male (Eden × (Eden × male Munsoniana)), 6- San Alba × (Thomas × (Eden × (Eden × male Munsoniana))), 3- San Alba × (muscadine seedling × (Eden × male Munsoniana)), 5- San Rubra × male (Eden × (Eden × male Munsoniana)), 3- San Rubra × (Eden × (Eden × male Munsoniana), 1- San Rubra × (Thomas × (Eden × (Eden × male Munsoniana))), 1- muscadine seedling × (Eden × (Eden × male Munsoniana)), 1- muscadine seedling × male (Eden × male Munsoniana), 1- muscadine seedling × (muscadine seedling × (Eden × (Eden × male Munsoniana))), 13- muscadine seedling × male (Eden × (Eden × male Munsoniana)), 1- muscadine seedling × (Eden × (Eden × male Munsoniana)), 2- muscadine seedling × (muscadine seedling × (Eden × (Eden × male Munsoniana))), 20- muscadine seedling × (muscadine seedling × (Eden × (Eden × male Munsoniana))), 3- muscadine seedling × (Eden × male Munsoniana), 1- (Eden × (Eden × male Munsoniana)) × male (Eden × (Eden × male Munsoniana)), 3- (James × white male) × (Eden × (Eden × male Munsoniana)), 2- (James × white male) × (muscadine seedling × (Eden × (Eden × male Munsoniana))), 1- James seedling × (muscadine seedling × (Eden × (Eden × male Munsoniana))), 1- muscadine seedling × male (Eden × (Eden × male Munsoniana)), 1- selfed seedling (James × (Eden × (Eden × male Munsoniana))), 3- selfed seedlings (Thomas × (Eden × (Eden × male Munsoniana))), 1- selfed seedling (muscadine seedling × (Eden × (Eden × male Munsoniana))), 2- selfed seedlings (muscadine seedling × (Eden × (Eden × male Munsoniana))). (All pollen parents were hermaphrodite seedlings unless designated as male.)

Vinifera grape varieties available for breeding work in United States Department of Agriculture experiment vineyards [8]

[Alphabetically arranged]

Ach-I-Soum, Affenthaler, Agadia, Agra Ash, Ak Saibe, Aibatly Isium, Ajmi, Ak-usum, Aldara, Aleatico, Alexandria, Alicante, Alicante Bouschet, Alnwick

[8] This list contains many names of Persian or other foreign origin that have no exact English equivalent and also includes some recent introductions that have not yet found a place in American grape literature. Such names are to be regarded as tentative and not necessarily authentic and final.

seedling, Alvarna, Amlachu, Aneb-el-Cadi, Angur Khalili, Angur Noir Grande, Apapnish White, Appley Towers, Aramon, Ascot Citronelle, Askaree, Asmi, Aspiran Noir, Atch Gau, Augulato, Awasarghua.

Baba, Bakator, Barbarossa, Barbera, Barducci, Bastardo, Beclan, Bellino, Bengi, Bermestia Violacea, Bicane, Black Alicante, Black Hamburg, Black Morocco, Black Prince, Black Seedless, Black Shahanee, Black Zante (South Africa currant grape), Blanc d'Ambre, Blaney White, Blauer Portugieser, Boal de Madeira, Bocalilla, Bolgnino, Bonarda, Boudelais, Bowood Muscat, Brustiano, Buaki, Buccleuch, Buckland Sweetwater, Buhirzi, Burger.

Cabernet Sauvignon, Calabrian, Calmette, Cannon Hall Muscat, Carignane, Castiza, Cefid, Ceskarg Charial, Chabach, Chali Sar, Chani Rouge, Chaouch blanc, Chaouch Rose, Charas, Chasselas Ciotat, Chasselas de Fontainebleau, Chasselas Rose de Falloux, Chasselas Rouge, Chasselas St. Bernard, Chaweesh, Child of Hall, Chirazi, Chauch Gris, Chauch Noir, Cinsaut, Cipro Nero' Clairette a Gros Grain, Coarna Neagra, Corazon de Cabrito, Corinthe a Gros Grain, Corinthe Rose, Coristano, Crabbs Burgundy.

Damas Rose, Danugue, Dattier de Beyrouth, Deis-el-A'anze, Diamond Jubilee, Directeur Tisserand, Dizmar, Doctor Hogg, Drnckusa, Dronkane, Duc de Malakoff, Duchess of Buccleuch, Duke of Buccleuch.

Emperor, Esandri, Eskari Riz, Etraire de l'Adhui.

Fajaumi Jaune, Faphly, Feher Szagos, Feher Som, Fintendo, Flame Tokay, Foster, Frankenthal Précoce, Fredericton.

Gamay de Bourgogne, Gamay Teinturier, Gewürz Traminer, Ghiliaki Krasnaya, Ghulabi Black, Ghulabi Red, Ghusaine, Golden Champion, Golden Hamburg, Goolabie, Gradiska, Grove End Sweetwater, Green Hungarian, Grenache, Gros Blanc de Lausanne, Gros Colman, Gros Guillaume, Gros Manzenc, Gros Verdot, Guadalupe.

Hebron, Hunisa, Hycales.

Imperial Blanc, Insolia Bianca, Italia Elqui.

J'bai, Johannisberger, Jubeili.

Kabasma, Kabbajuk, Kadarka, Kahalillee, Kharashani, Kara-Usum, Karoo Belle, Kasufi-Dakar, Kasufi inti, Katta-Kurgan, Kechwechi Bleue, Kechwechi Rouge, Keropodia, Kandihar, Khasseyne, Khudud-ul-Banat, Kishmish daba, Kölner, Koptchak, Koshu, Ksil-isjum, Kurdi, Kurtelaska.

Lady Downe, Lady Hastings, Lady Hutt, Lal Cefid, Lal Guermez, La Mollar, Larien, Leani Zolo, Lignan Blanc, Lore Koche, Luglienga Nera.

Macaboc de Satin, Madeleine Angevine, Madeleine d'Ambre, Madeleine Royale, Madresfield Court, Malaga, Malaga Rose, Malakoff Isjum, Malvasia de Brogliana, Malvasia Rosaria, Malvasia Rovasenda, Mamelon, Mantuo di Pilo, Marmora, Marascina, Marzamina Genuina, Maskah (Nos. 24772, 24774, 24775, 24776, 24781, 24782, 24783, 24784, 24785, 24786, 24787, 24788, 24792, 24793), Mataro, Melhi Khany, Melton Constable, Meslier Hatif, Meunier, Miksasi, Millenium, Mission, Monake, Mon. Deludda, Mondeuse, Monukka, Mourastel, Mourisco Bianca, Mourisco Preto, Mrs. Pince, Mskhali, Mukhkh-ul-Baghl, Muscatel Commune, Muscat Bonod, Muscat Capusines, Muscat de Frontignan, Muscat Gros Noir Hatif, Muscat Hamburg, Muscat Noir d'Hongrie, Muscat Noir Precoce, Muscat Rose, Muscat Talabot.

Nasa Valentiana, Nebbiolo, Nebbiolo Bourgu, Nebbiolo Fino, Negro Amaro, Negrara di Gattinara, Negra Elqui, Negra Nero, Nimrang.

Ohanez, Ojo de Liebre, Olivette Blanche, Olivette de Vendemain, Olivette Noire, Opiman.

Pagadebito, Palarusa, Palomino, Panariti, Parc de Versailles, Pastilla Elqũi Paykanee Razuki, Perle de Csaba, Pedro Ximines, Perle Imperial Blanche, Perruno, Persian (no number), Persian (no tag), Persian (nos. 21–26), Petit Syrah, Petit Verdot, Peverella, Piment, Pince Muscat, Pineau de Chardonnay, Pineau Noir Epernay, Pinot St. George, Pirovano, Pizzutella, Plavai, Poulsard, Pomology No. 68091, Prince of Wales, Prune de Cazouls, Purple Damascus.

Quagliano, Quanque.

Red Hanepoot, Refosco, Rka-tzital, Robin Noir, Rodites, Ronde Weisse, Rose d'Italia, Rose of Peru, Rothgipfler, Rousseau, Royal Ascot.

Schach-I-Soum, Sahibi, Sahibi Charial, Saidi, San Giovetto, Satin Blanc, Sauvignon Blanc, Sauvignon Vert, Schiradzouli Blanc, Schiradzouli Violet, Semillon, Serektia, Serine, Servan Blanc, Servan Rose, Schaani, Shahmani, Shakaifi, Shanzi,

Shirshira, Shuvarghani, Sicilien, Slankamenka, Souvenir du Congrès, St. Laurient, St. Macaire, Sufetha, Sultana, Sultanina, Sultanina Rosea, Suri, Sylvaner.

Tadone, Tagonte Rouge, Tanfi Rose, Tannat, Tavris (no. 27963, 30467), Teneron de Cadenet, Tifafihi Ahmer, Tinta Amerella, Tinta Cao, Tinta de Madeire, Trentham Black, Trojka, Trousseau.

Ubeide, Umagum, Uva de Casta.

Valandova, Valdepenas, Veltliner, Verdel, Vermentino, Vigne de Zericho.

Wälschriesling, Werme, West Prolific, White Corinth, White Frontignan, White Nice, White Tokay, Wilmot No. 16.

Zabalskanski, Zeine, Zenkoji, Zinfandel, Zinzillosa.

Grape rootstock varieties available for breeding work in United States Department of Agriculture experiment vineyards

[Alphabetically arranged]

Adobe Giant; (*Vitis aestivalis* × *monticola*) × (*V. riparia* × *rupestris*), no. 554–5; (*V. aestivalis* × *rupestris*) × *riparia*, no. 227; Alicante Bouschet × *V. cordifolia*, no. 142–B; Alicante Bouschet × *V. riparia*, no. 141–A; Aramon × *V. riparia*, no. 143–A; Aramon × Rupestris Ganzin (nos. 1, 2, 9); Arizonica Phoenix; Australis.

Barnes; *Vitis berlandieri* (nos. 1, 2); Berlandieri Lafont, no. 9; *V. berlandieri* × *riparia* (nos. 33 E. M., 34 E. M., 157–11, 420–A, 420–B); (Bourrisquou × *V. rupestris*, no. 601) × Calcicola, no. 13205.

Cabernet × *V. berlandieri*, no. 333 E. M.; Cabernet × Rupestris Ganzin, no. 33–A; Chasselas × *V. berlandieri*, no. 41–B; (*V. cinerea* × *rupestris*) × *riparia*, no. 229; Columbaud × *V. riparia*, no. 2502; Constantia; *V. cordifolia* × *riparia*, no. 125–1.

DeGrassett; Dog Ridge.

Hotporup.

Joly; Judge.

V. monticola × *riparia* (nos. 18804, 18808, 18815); *V. monticola* × *rupestris;* Motley; Mourvedre × *V. rupestris* (nos. 1202, 1203).

Pinot Bouschet × *V. riparia*, no. 3001; Pinot × *V. rupestris*, no. 1305; Ponroy.

Ramsey; Riparia Gloire; *V. riparia* × *berlandieri*, no. 161–49; *V. riparia* × (*cordifolia* × *rupestris*), no. 106–8; Riparia Grand Glabre × (Aramon × *V. rupestris*), no. 4110; *V. riparia* × *rupestris* (nos. 101, 101–14, 108–103, 3306, 3309); *V. riparia* × *V. rupestris*, Jaeger; *V. riparia* × (*rupestris* × Aramon), Jaeger, no. 201; *V. riparia* × Rupestris Ramond; Rupestris des Causettes; Rupestris des Semis, no. 81–2; Rupestris Ganzin; Rupestris Le Reux; Rupestris Martin; Rupestris Metallica; Rupestris Mission; Rupestris Othello; Rupestris Pillans; Rupestris St. George; *V. rupestris* × *berlandieri* (nos. 219–A, 301–A, 301–B, 301–37–152); *V. rupestris* × Chasselas Rose, no. 4401; *V. rupestris* × *cinerea; V. rupestris* × *cordifolia*, no. 107–11; *V. rupestris* × (*cordifolia* × *rupestris*), no. 202–5; *V. rupestris* × Azemar, no. 215; *V. rupestris* × Petit Bouschet, no. 503; *V. rupestris* × Petit Bouschet, no. 504; *V. rupestris* × *riparia*, no. 108–16.

Salt Creek; Solonis Ordinaire; Solonis Robusta; Solonis × (*V. cordifolia* × *rupestris*), no. 202–4; Solonis (*V. longii*) × Othello ((*V. riparia* × *labrusca*) × *vinifera*), no. 1613; Solonis × *V. riparia* (nos. 1615, 1616).

Taylor Narbonne; Tisserand.

Vermorel; Viala; Viala × *V. riparia; V. candicans.*

York × Rupestris Ganzin, no. 212.

Direct-producing grape varieties available for breeding work in United States Department of Agriculture experiment vineyards

Bourrisquou × *Vitis rupestris* (nos. 601, 603, 109–4, 3907, 4306, 4308).

Carignane × *V. rupestris* (nos. 404, 501); Castel (nos. 1028, 19002); Clairette Dore Ganzin; Couderc (nos. 101, 201, 503, 704, 3701, 4401, 28 × 112, 71–06, 71–20, 74–17, 82–32, 4 × 61, 85 × 113, 87 × 115, 124 × 30, 132–11, 199–88, 241–55, 267–27, 272–60).

Pardes.

Seibel (nos. 1, 2, 14, 29, 38, 60, 70, 78, 80, 128, 156, 209, 215, 334, 1004, 1070, 1077, 2010, 2029, 2033, 2043, 2044, 2056).

IMPROVEMENT OF STONE FRUITS

F. P. CULLINAN, Senior Pomologist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry[1]

THE beautiful and delicious varieties of peaches, plums, cherries, and apricots that make up the group of stone fruits as we know them today are undoubtedly vastly different from their early progenitors. Down through the centuries many wild species and varieties have been selected by man in his search for new food supplies and a better diet. Just how long this slow process of improvement of the various kinds of wild fruit has been going on, history does not relate. As civilization progressed we know that many of these wild fruits were taken from their native homes and distributed to new locations where there were new soils and new climatic conditions. In these new environments certain modifications occurred in size of tree and in size, shape, color, and flavor of fruit. Many trees perished in the new environments. Perhaps only a few survived the vicissitudes of climate in some of the regions into which they were taken. Through these early chance selections, however, a beginning was made in the improvement of the stone fruits.

Stone fruits are now grown in all parts of the Temperate Zone in the Northern Hemisphere. In the United States the culture, production, and sale of these fruits constitute a great industry. In 1931, the peak year of peach production, the commercial crop was over 76½ million bushels. According to the census of 1935, the country produced in the previous year about 45 million bushels of peaches, over 23 million bushels of plums, and 5 million bushels of cherries. Peaches, plums, and apricots in the fresh, canned, and dried state are consumed in large quantities in this country and abroad. About 200,000 tons of peaches are dried in the United States annually. California alone produces about 75 percent of the world output of dried prunes. Cherries are commercially important as fresh, canned, and frozen products. There is little wonder that such a great industry should demonstrate weaknesses in many of our long-cherished varieties of home-grown fruits. We might imagine that after all these years of selection and discovery of new sorts, we would have reached perfection. Unfortunately, this is not the case; in fact, it may be said that

[1] The author wishes to acknowledge his indebtedness to the following workers engaged in stone-fruit breeding in this country and abroad for their kind cooperation in furnishing information on the work in progress in their respective States and in furnishing lists of varietal and species material available for breeding studies: W. A. Alderman, Minnesota; J. S. Bailey, Massachusetts; M. A. Blake, New Jersey; M. J. Dorsey, Illinois; N. E. Hansen, South Dakota; F. W. HofMann, Virginia; Stanley Johnston, Michigan; T. J. Maney, Iowa; W. P. Tufts, G. L. Philp, E. C. Hughes, and J. W. Lesley, California; Richard Wellington, New York; S. H. Yarnell, Texas; A. F. Yeager, North Dakota; W. F. Wight, U. S. Bureau of Plant Industry, Palo Alto, Calif.; W. P. Baird, U. S. Northern Great Plains Field Station, Mandan, N. Dak.; E. F. Palmer and G. H. Dickson, Vineland, Ontario, Canada; H. Wenholz, New South Wales Department of Agriculture; and M. Ch. Miedzyrzecki, Ain Taoujdat, Morocco.

the work of improvement has just begun. We must continue the search for superior fruits, locating and studying the best raw materials, and then using the methods available to the plant breeder to combine desirable characters in a superior progeny.

BOTANY OF THE STONE FRUITS

Before attempting to consider the progress made in improving the varieties of stone fruits, a few words should be said about the botany of these fruits in general.

Botanists have classified the stone fruits into several species. While there has not been entire agreement as to the number of these species, most botanists place them in the great genus *Prunus* in the rose family (Rosaceae); others, however, separate the peach and its close relatives as the genus *Amygdalus*. The fruit develops from a one-celled ovary the wall of which ripens with a fleshy, juicy exterior, making up the edible part of the fruit, and a hard interior, called the stone or pit. The seed is contained in the stony portion.

But while these fruits have enough in common to be grouped in the same genus, they are quite different in many fruit, flower, and tree characters. When the fruits are ripe the flesh of some varieties parts readily from the pit. Such fruits are spoken of as freestones. Other varieties and species, for example, the canning cling type of peaches, are clingstones; that is, the flesh adheres to the stone. The individual fruits may be smooth, as in the apricot, nectarine, plum, and cherry, or hairy, as in the peach. They vary in size, color, and shape

THE *kind of search in which the breeder of peaches is engaged may be illustrated by the Elberta. This is the leading commercial peach in the United States today. It originated in Marshallville, Ga., in 1870, and in the 67 years since that time no better peach has been found, when all characteristics are considered. Yet in quality the Elberta does not rank as high as some other peaches, and the tree and the blossom buds are not sufficiently resistant to low winter temperatures. By suitable crosses, varieties have been developed that have better quality and more cold resistance in the bud; but these in turn are not adapted to so many different growing regions as the Elberta. Again, seedlings of Elberta have been found that ripen earlier than the parent variety and are better in quality and more attractive. It would seem possible, then, to develop a variety that would be a distinct improvement over Elberta, yet possess the valuable characteristics that have given the Elberta preeminence. Such an achievement would be a major contribution to fruit culture in the United States.*

with varieties and species. The flesh may be yellow, green, white, or red, or show various combinations of these colors. The stones or pits of the peach are rough and grooved, those of the plum and cherry relatively smooth, those of the apricot somewhat intermediate.

The flowers of the different stone fruits are quite characteristic for the respective groups. In the peach and the apricot they are borne singly, arising from one to three separate buds at a node. They are practically without stems in the peach, and nearly so in the apricot. They are on long stems in the cherry and on only moderately long ones in the plum, but in both these fruits the flowers are borne in clusters. The flowers of the edible plums are white or nearly so, while those of the peach and the apricot may be white, pink, or reddish.

As will be pointed out later, hybridization between some of the species of stone fruits is practically impossible.

METHODS OF BREEDING

The technique of stone-fruit breeding is not greatly different from that employed with other deciduous fruits. The essential operations are (1) collecting pollen to be used in the crosses, (2) emasculation of the flowers, (3) pollination, or the actual transfer of pollen to the stigmas of the pistil, (4) bagging, or protecting flowers from foreign pollen, (5) protecting fruit that has set, and (6) growing the seedlings for testing and study of the progeny.

Much of the breeding work with stone fruits is carried on with trees growing in the orchard. This has its drawbacks as well as many advantages. Blossom buds, flowers, or young developing fruits may be killed by cold. Under such conditions the continuity of breeding work is interrupted and a year's time is frequently lost. To avoid this difficulty, particularly in the regions of unfavorable climate, it has been found satisfactory to grow the trees in tubs or pots in the greenhouse. Emasculation and pollination can thus be carried on under controlled temperature. Since it is necessary for most stone fruits to have sufficient cold to bring them out of the rest period, the trees in tubs must be removed from the greenhouse in late summer or fall and placed out of doors or in a cool storage place. They may be brought back to the warm greenhouse by the middle of January, and the trees should then bloom in 3 or 4 weeks. While greenhouse trees do not reach the large size of those growing in the field and consequently do not produce as many blossoms, sufficient material can usually be obtained for certain crosses and for genetic and cytological study. In some cases it may be the only way blossoms can be produced for breeding work.

In obtaining pollen to be used in breeding it is usually necessary to collect shoots of the male parents desired and force the blossoms in a greenhouse or warm room in order to have the pollen available when the flowers on the tree are ready for pollination. Care should be taken, of course, that no foreign pollen is introduced by bees or other insects. When the flowers have opened, the anthers may be plucked off by running the filaments through a comb or some similar instrument that will lift off the anthers, which may then be placed in suitable containers to dry at room temperature of 65° to 70° F. When dry they break open and the pollen can be easily crushed out. The pollen

should be stored in a dry, cool place in vials or small boxes, from which it may be used directly when the crosses are made. It is convenient to leave a small camel's-hair brush in each container to use in the transfer of pollen.

The structure of the flowers of the peach and other stone fruits permits rapid emasculation. The stamens and the single pistil are enclosed under the folded petals. As the blossom expands from the bud scales, the calyx pushes up, carrying the nonexpanded leafy floral structures, forming a cup around the ovary. The long style of the pistil grows up through the stamens and under certain conditions may even push through between the petals before they expand (fig. 1). In the technique of emasculating, the calyx cup is easily cut with the nails of the thumb and first finger, and the entire corolla with its three rows of stamens attached may be lifted from the flower, leaving the pistil undisturbed. Early workers used sharp-pointed tweezers or scissors to cut the calyx cup, but the fingernail method is more rapid. With varieties of peach that are pollen-sterile, or varieties of plums and cherries that are self-unfruitful, emasculation is unnecessary in ordinary hybridization. A small percentage (0.5–0.8) of set is sometimes obtained in selfing self-unfruitful varieties. While this is a negligible amount in variety breeding, it should not be overlooked in cytological studies.

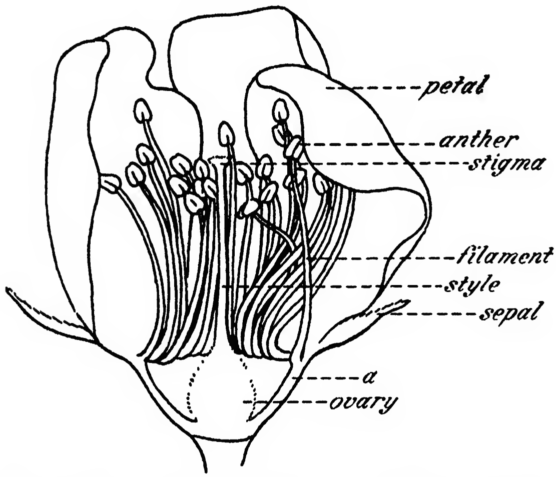

Figure 1.—Section through a peach flower showing arrangement of floral parts. By pinching through the calyx cup at *a* with the thumb and first finger, sepals, petals, and stamens are all removed in one operation, leaving the single pistil.

If emasculation is done just before the petals open (fig. 2)—which is just before any pollen that might cause selfing has been shed—the pollen of the parent to be used in the cross may be applied to the stigmas at once. Where a large number of pollinations are made on a single tree, it is frequently convenient to emasculate all the blossoms before pollinating. With the aid of the camel's-hair brush, from the pollen container a large number of flowers can be pollinated in a short time. Some workers prefer to use the tip of the finger, to which the pollen will adhere, and apply the pollen by touching the stigmas. Care should be taken to remove all pollen grains of one variety or strain from the finger before dipping into a container of another variety. The individual blossoms, single shoots, or entire branches that have been pollinated with a single pollen variety should be carefully labeled with full data on a tag or label that will remain until the fruit is harvested.

Figure 2.—Flower buds of peach (left) showing ideal stage for emasculation. Within 24 hours with temperatures of 70° to 75° F. the flowers will open as shown on right.

Protecting flowers after pollination is important. The method generally used is to tie a glassine or paper bag over the end of the branch bearing the pollinated flowers (fig. 3). Sometimes two or three flowers may be enclosed in a single bag. With some of the stone

fruits, particularly the peach, this method has not been entirely satisfactory, especially where the breeding work is done in the orchard. The relatively long style or stalk of the pistil is easily broken if the bag blows against it (fig. 4) causing loss in bagged flowers. It is necessary, however, to use some method of protection where only a

Figure 3.—When only a few blossoms on the tree are to be pollinated it is necessary to protect the flower from foreign pollen. A heavy paper bag or some cover not easily collapsed by the weather is necessary to prevent injury to the pistil.

few flowers on a tree are pollinated. A very heavy grade of paper bag with sufficiently sturdy basal folds to hold the sides out from the flower when the bag is inverted over the branch and tied is desirable to reduce the injury to a minimum. When large numbers of crosses are made, and when no special genetic or cytological studies are undertaken, it is doubtful whether peach flowers need to be protected, particularly if an entire branch or tree has been emasculated. Bees or other insects in visiting the emasculated flowers rarely touch the

stigmas and thus do not introduce foreign pollen. If an entire tree is emasculated for a large number of crosses, a tent built over the tree will prove satisfactory not only as a means of protection for the emasculated flowers but for insuring a large set of fruit under unfavorable weather conditions.

After fertilization of the ovules has taken place (fig. 5) and the style begins to darken and wither, the protecting paper bag is removed and an open-mesh bag of coarse cheesecloth or heavy net is placed over the end of the branch to protect the developing fruit. If the fruit drops off at maturity it will be held in the bag. Where the entire tree has been emasculated and tented, or where a number of branches on the tree have been pollinated without bagging, it is necessary to harvest the fruits before they fall.

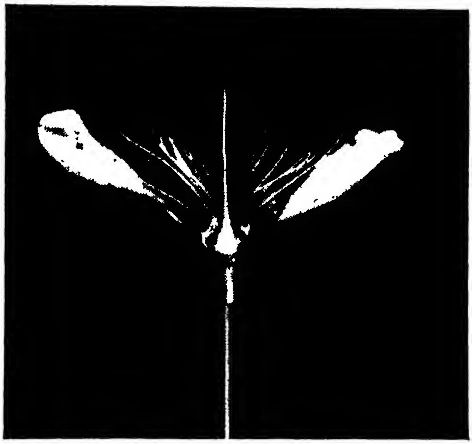

Figure 4.—A peach flower after fertilization, showing the pistil with its long style and the enlarging hairy basal portion, the ovary, which becomes the fruit. In the cherry, plum, apricot, and nectarine the fruit develops similarly from a single hairless ovary.

The stones are removed from the harvested fruit and are allowed to dry in a place free from molds and fungus contamination. Seeds of stone fruits require an after-ripening period of 2 to 3 months at low temperatures before they will grow. They are usually soaked for several hours and then placed in moist sand out of doors during the winter, or, preferably, they may be held for 2 or 3 months in a refrigerator or cold storage at about 40° F.

To insure a high percentage of seedlings in the case of valuable material, the best method is to remove the pits from the cold box, crack them, and remove the seeds. The seed coats are then removed and the young embryos sterilized in hypochlorite solution or some similar disinfectant and placed in small bottles on sterile nutrient agar to grow. When the young seedlings are rooted and a few inches tall, they may be transplanted from the culture bottles to pots in the greenhouse and later removed to the field or nursery row. The more common method of growing the seed is not to remove the seed coat but to plant the seed directly in pots in the greenhouse or in the nursery. Sometimes the pits are not cracked but are planted directly in the field in the fall when out-of-door temperatures will bring about the proper chilling required to insure growth of the seeds in the spring.

A great obstacle in stone-fruit breeding is the difficulty in getting the seeds of some crosses to resume growth. Many hundreds of seeds of crosses of sweet cherry, early-ripening varieties of peach, and other stone fruits have been planted, but no seedlings grew from apparently normal seeds. It is believed that planting the seeds on sterile nutrient

agar will be helpful. At the present time, however, there are stubborn seeds of early-ripening varieties of peach and cherry that will not grow even though given the agar-culture treatment. Many such varieties possess desirable characteristics, but they cannot be used as female parents until some method is found to obtain germination of the apparently normal seed they produce.

To economize space the young seedlings are usually planted in test blocks in rows 10 feet apart, with the trees 5 feet apart in the row, which is about as close as cultural operations will permit. At least

Figure 5.—**Peach flowers after emasculation and fertilization. The single pistil (*A*) is normal, but occasionally, in some varieties and under certain nutritional conditions, two (*B*) or more pistils (*C*) may develop in a single flower.**

3 or possibly 4 years must elapse before fruit characters can be studied. If it is decided to hasten the fruiting of the progeny, buds or scions can be taken from the seedlings when they are large enough and grafted into branches of bearing trees. In general, budding has proved a more satisfactory method for top-working peach than grafting. In California, however, grafting has proved very satisfactory in the hands of experienced men when dormant scions were placed early in the spring in the cut-back branches of trees 4 to 8 years old. Fruit may be obtained in 2 years from budding, and sometimes in 1 year from grafts. Where tree characters of the seedlings are to be studied, this information is best obtained by leaving them in the field for some years after first fruiting.

Under the most favorable conditions it requires about 5 years from the time the cross is made until a preliminary reading is obtained from the seedling and trees can be propagated for testing in the orchard. If we assume the average life of a peach tree to be about 15 years, then it will be about 20 years before full evaluation can be made of the lifetime merits of a variety. Frequently a much longer time elapses before the value is determined, because of the fact that new varieties are not tested promptly under widely varying soil and climatic conditions.

PEACHES

Early History

The original home of the peach (*Amygdalus persica* L. or *Prunus persica* Batsch.) was thought to be Persia, since this fruit was doubtless introduced into Greece from that country shortly after the beginning of the Christian Era. De Candolle concludes, however, that the peach has never been truly wild in Persia. Botanists agree that the peach is wild in China. The late Frank N. Meyer, explorer of the United States Department of Agriculture, reported finding many wild peaches in China, the fruits of which are inedible, being small and hairy, hard, and with a sourish flesh (*17*).[2] The peach has also long been cultivated in China. It was written about some 2,000 years before its introduction to the Roman world. Reference to the "tao", meaning peach, has been found in the writings of Confucius in the fifth century B. C. and in the Ritual in the tenth century B. C.

There is evidence that the peach reached France and possibly Spain at about the time it was introduced into Greece. From southern Europe it spread to northern Europe, possibly the greatest spread taking place from France. In more recent times France has been an important nursery center, and in the fifteenth and sixteenth centuries nursery trees were sent from France and disseminated through England, Belgium, the Netherlands, and Germany.

Few other fruits are grown under such varied conditions and over such extended areas as the peach. Once a wild inhabitant of China, it is now cultivated in every part of that vast country. Extensive plantings of the peach occur in Turkistan and Persia. It is not surprising, therefore, that early writers regarded Persia as the original home of the peach, as is suggested by the species name *persica* later given it. Peaches thrive in all parts of southern Europe and are grown in sheltered places in the northern latitudes. In the United States the peach found such congenial surroundings that it spread rapidly and widely, leading botanists three centuries later to believe it was native to this country. Today peach varieties are found growing in practically every State of the Union. While the fruit is not grown commercially in regions that are subject to low winter temperatures, some varieties or seedlings are able to withstand the winter temperatures in the colder parts of the country.

Because of the general distribution of the peach in Europe, Asia, South Africa, Australia, South America, and the United States, there has been a general selection of varieties best adapted to the various regions and climatic conditions, as well as to the preferences of consumers. Through this process of selection and hybridization peach varieties with widely differing characteristics have been developed and propagated. Some of the wide differences are so marked that botanists have been inclined to separate the peach into races and, in a few instances, species.

American pomologists (*25*) in the past century tried to divide peaches into four groups or races: (1) The Persian race, brought to North America by the early settlers, best represented by varieties

[2] Italic numbers in parentheses refer to Literature Cited, p. 746.

of the Crawford group; (2) the north China or Chinese Cling race, characterized by large fruits with tender skin and flesh, vigorous tree growth, and abundant and regular bearing, and including such Chinese varieties as Chinese Cling, Chinese Free, and later descendants Belle and Elberta; (3) the south China race, sometimes called

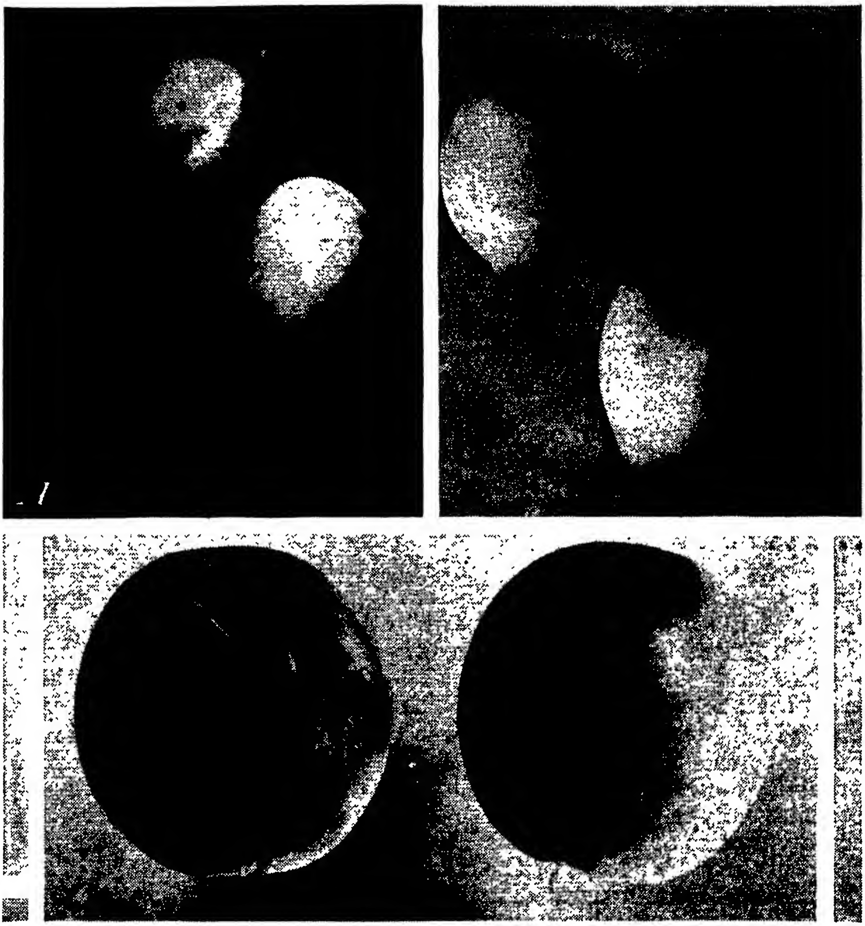

Figure 6.—Shapes of different types of peaches that may be used in breeding: *A*, Peento, or so-called saucer peach of the Gulf States; *B*, the honey peach of Florida and Texas, represented by varieties such as Imperial and Honey; *C*, peach of the Chinese Cling type, representing most of our present-day commercial freestone and canning cling varieties.

the Honey, represented by varieties that bear small, oval to pointed, white-fleshed fruits with a peculiar honey-sweet flavor, and adapted in the United States only to some subtropical sections; (4) the Peento race, a warm-climate type with trees inclined to be evergreen and to bear fruits that are much flattened endwise, white-skinned and white-fleshed, and sweet to very sweet. However, all varieties hybridize

freely, and there has been so much crossing between the groups that it is practically impossible to classify many of our present yellow- and white-fleshed varieties on this basis (*16*) (fig. 6).

The nectarine was formerly thought to be a different species from the peach. It is now known that the nectarine is simply a smooth-

Figure 7.—The beginning of commercial peach growing. The early settlers planted fruit trees near the homestead. The home orchard frequently gave place to large commercial plantings.

skin peach. The trees differ in no respect from the peach, and it is impossible to tell a peach tree from a nectarine tree. The leaves are the same. The fruits and seeds have essential characteristics in common. In short, the only difference between the peach and the nectarine is the absence of hairs in the latter. Nectarines are known to have come from peach seeds, and vice versa.

Commercial Peach Growing and Its Stimulus to Variety Improvement

Commercial peach growing in the United States began early in the nineteenth century (fig. 7). Large orchards were planted in Maryland, Delaware, and New Jersey. Prior to this time thousands of peach trees, all seedlings, were planted by growers. Many of the varieties grown in those early years were apparently better suited for making brandy than for general consumption as canned or fresh fruit. While the art of budding and grafting had been known for a long time, it was not until early in the nineteenth century that large commercial orchards of varieties propagated from clons were used.

TABLE 1.—*Fifty varieties of peach grown commercially in the United States during the past 25 years*

Variety	Place of origin	Date of origin	Originator or introducer	Color of flesh	Firmness of flesh [1]	Stone free or cling	Ripening date [2]	Quality
Admiral Dewey	Vineyard, Ga	1899	J D Husted	Yellow	Soft melting	Semifree	July 15–23	Good
Alton	Denison, Tex	1899	T V Munson	White	do	do	Aug 3–10	Do
Arp	Arp, Tex	1897	C P Orr	Yellow	do	Semicling	Early	Very good
Belle	Marshallville Ga	18[illegible]0	L A Rumph	White	Melting	Free	Aug 16–20	Good
Brackett	Augusta, Ga	1912	J P Berckmans	Yellow	do	do	Aug 29–Sept 1	Do
Carman	Mexia, Tex	1889	J W Steubenrauch	White	Soft melting	Semifree	July 31–Aug 5	Do
Chairs	Anne Arundel County Md	1880	Franklin Chairs	Yellow	Melting	Free	Late midseason	Excellent
Champion	Nokomis Ill	1880	I G Hubbard	White	Soft melting	do	Aug 17–22	Do
Chili	Chili N Y	1845 (?)	Pitman Wilcox	Yellow	Melting	do	Sept 8–12	Fair
Chinese Cling	Shanghai, China	1850	Imported by Charles Downing	White	do	Cling	Aug 25–29	Good
Climax	Florida	1886	G L Taber	do	Soft melting	Semifree	Late	Do
Crosby	Billerica, Mass	1876	Mr Crosby	Yellow	Melting	Free	Late midseason	Do
Early Crawford	Middletown, N J	1820 (?)	William Crawford	do	do	do	Aug 17–20	Very good
Early Elberta	Kaysville, Utah	1908	Sumner Gleason, Stark Bros Nursery	do	do	do	Midseason	Good
Early Wheeler	McKinney Tex	1906	E W Kirkpatrick	White	Nonmelting	Cling	July 11–20	Fair
Elberta	Marshallville Ga	1870	S H Rumph	Yellow	Melting	Free	Aug 21–27	Good
Engle	Paw Paw, Mich	1875	C C Engle	do	do	do	Aug 24–Sept 3	Do
Eureka	Louisiana	1870	Unknown	White	Soft melting	Semifree	July 27–Aug 5	Do
Foster	Medford, Mass	1857	J T Foster	Yellow	Melting	Free	Late midseason	Very good
Frances	Texas	1895	L T Sanders	do	do	do	Sept 3–8	Good
Gaume	Live Oak, Calif	1913	Louis Gaume	do	Nonmelting	Cling	Late midseason	Do
Gold Drop	Michigan	Unknown	George W Griffin	do	Melting	Free	Sept 8–10	Do
Greensboro	Greensboro, N C	1891	W G Balsey	White	Soft melting	Cling	July 13–18	Do
Hale Early	Ohio	1850	Mr Moss Introduced by Hale and Jewett Nursery	do	do	Semifree	July 23–28	Do
Heath Cling	Unknown	1760–70(?)	Unknown	do	Melting	Cling	Sept 22–27	Do
Hiley	Marshallville, Ga	1886	Eugene Hiley	do	do	Free	Aug 8–14	Very good
Illinois	North Alton, Ill	1910	E H Riehl	do	do	do	Aug 17–25	Do
Iron Mountain	New Jersey	1890	Unknown	do	do	do	Sept. 21–25	Fair to good
J H Hale	South Glastonbury Conn	1912	J H Hale, W P Stark	Yellow	Firm melting	do	Aug 23–30	Good
Kalamazoo	Kalamazoo, Mich	1869	J N Stearns	do	Melting	do	Aug 8–31–Sept 3	Do
Krummel	St Louis, Mo	1895	Mr Krummel	do	do	do	Sept 23–27	Do
Late Crawford	Middletown, N J	1815(?)	William Crawford	do	do	do	Sept 5–9	Very good
Lemon Free	Ohio	1885	Unknown	do	do	do	Sept 12–19	Good
Lola	Mexia, Tex	1876	J W Steubenrauch	White	do	Semifree	Medium early	Do
Lovell	Winters, Calif	1882	G W Thissell	Yellow	do	Free	Late midseason	Do
Mayflower	North Carolina(?)	Unknown	Unknown	White	Soft melting	Cling	June 19–30	Fair
Mountain Rose	Morristown, N J	1851	Dr Marvin	do	Melting	Free	Aug 16–19	Good
Oldmixon Free	Unknown	1835	Sir John Oldmixon	do	do	do	Sept 3–8	Do
Muir	John Muir farm, Silveyville, Calif	1890	G W Thissell	Yellow	do	do	Aug 19–25	Do

Pallas	Augusta, Ga	1878	L E Berckmans	White	do	do	Aug 22-26	Do
Peento	China	1828	William Prince	do	do	do	Medium early	Do
Phillips	Sutter County, Calif	1880	Joseph Phillips	Yellow	Nonmelting	Cling	Sept 12-19	Do
Paloro.	Gridley, Calif	1912	Frank Dixon	do	do	do	Aug 22-26	Do
Prolific	Michigan	1890	Greening Bros	do	Melting	Free	Aug 25-Sept 1	Do
Rochester	Rochester, N Y	1900	Heberle Bros	do	do	do	July 30-Aug 5	Excellent
St. John.	Unknown	1860(?)	Unknown	do	do	do	Aug 5-10	Do
Salwey....	Surrey, England	1844	Colonel Salwey	do	do	do	Late	Good
Stump	New Jersey	1825	Unknown	White	do	do	Sept 3-8	Very good
Triumph	Vineyard Ga	1895	J T Husted	Yellow	do	Semifree	July 15-27	Good
Tuskena (Tuscan)	Mississippi	1873	Unknown	do	Nonmelting	Cling	Early midseason	Do

[1] The terms "melting" and "nonmelting" are used to denote the degree of softness of the flesh of ripe fruits All freestones have either firm or soft melting flesh, and some early ripening clingstones (Greensboro) have soft, watery, melting flesh, while the flesh of clingstone varieties of the commercial canning type, such as Phillips, have firm nonmelting flesh

[2] The ripening dates are those for the U S Department of Agriculture orchard at Beltsville, Md, in 1936, a normal season Where the variety listed did not fruit, the general season is indicated as early or midseason

As the commercial industry spread, there was always a demand for varieties that would succeed best under various soil, climatic, and other environmental conditions occurring in the different peach-growing sections. In northern regions growers were interested in varieties hardy in wood and bud to withstand low winter temperatures, while in the more southern latitudes they were interested in varieties that would stand summer droughts and high temperatures and with fruit that would retain its firmness during shipment to distant markets. Then came the scourge of disease and insect troubles—peach yellows, leaf curl, brown rot, curculio, and the peach-tree borer. What varieties, if any, would prove most resistant to these troubles?

During the period 1850 to 1900 a large number of varieties were selected from seedlings as worthy of introduction. The list of 50 varieties given in table 1 contains the names of many that still have an important place in the peach sections of the country. They also served as parents for varieties introduced during the last 20 years. The dates of origin of these varieties cannot be accurately obtained in all cases. They are approximately correct and are given to show the length of time the variety has been under orchard test.

It will be noted that the geographical origins of these varieties include nearly all of the States east of the Mississippi between the Great Lakes and the Gulf. Peach growing as an industry was truly widespread in the United States by the end of the nineteenth century. The need for new varieties to replace those that had been under trial was apparent during the period from 1900 to 1910. This was principally due to the fact that peach growing was rapidly developing into an industry for specialists. When the business of peach growing had developed to a point where it was necessary to ship the crop to consuming markets several hundred miles from the orchards, varieties had to be chosen that would stand up in transit and compete successfully with varieties from other sections on the market at the same time. The freeze of 1899 had wiped out many orchards in the North and emphasized the need for varieties that would withstand cold for the commercial orchards of the future. More recent freezes of the winters of 1917–18, 1933–34, and 1935–36 have reemphasized the importance of developing varieties for the North that are more cold-resistant than many now being grown.

Work of Private Breeders in the United States

During the last 30 years there has been an increasing recognition by peach growers of the need of originating new varieties better adapted to meet local requirements in various regions. This is well illustrated by the more recent work of J. W. Steubenrauch, of Mexia, Tex., who developed the Carman variety from pits planted in 1889. It is one of many important commercial peach varieties originated in Texas during the period 1850–1900. Mr. Steubenrauch, now 84 years old, summarized his work in a letter on May 13, 1936.

He planted his first orchard of peaches in central Texas in 1879. There were many kinds available to the growers, mostly what were then called Indian peaches, some good, but not very suitable for general markets. Recognizing the need for varieties of the best quality ripening from early to late season, he bought many trees of new

varieties from various parts of the country. In the course of a few years he had 100 or more distinct varieties growing in his orchard. From this number there were not more than about 10 that would be called good varieties for that period, mostly suitable for home use. Among a lot of Elberta trees planted in 1884, he found one tree that he considered superior to all the rest, producing finer fruit more regularly. Having a fine later peach that was part Indian stock, named Belle October, he decided to bud from the fine Elberta and Belle October parents on a single stock away from all other peach trees. From the two varieties blooming together with bees as pollinating agents, he obtained fruit and seeds of the early and late varieties.

Planting the seeds from the best peaches of both varieties, he produced some fine new seedlings in season from the time of Elberta till late in October. One of the leading ones is the Frank, which was named for Frank P. Holland, publisher of Farm and Ranch. This peach bore a heavy crop again in 1936, making 32 years of continuous annual production. Mr. Steubenrauch describes this variety as a fine yellow-red cling, ripening in the middle of August in central Texas.

In addition to the Frank he produced six others that he considers fully as good. These are Tena, Lizzie, Liberty, Anne, Barbara, and Katie.

These varieties, which have been tested in southern latitudes as well as in some of the Northern States, have demonstrated superior germ plasm and are worthy of note for possible use by breeders of peaches.

The man who discovered and introduced the variety that took the lead in commercial peach production in this country from 1910 up to the present was the late S. H. Rumph. He produced the Elberta from a seed of Chinese Cling planted at Marshallville, Ga., in 1870. Curiously enough, another seed reported to have come from the same Chinese Cling tree, planted in the same year by S. H. Rumph's brother, L. A. Rumph, also of Marshallville, Ga., gave rise to the variety called Belle of Georgia. Today these two are still among the leading commercial varieties. They are of particular genetic interest because the Elberta, a yellow, and the Belle, a white, are reported to have come from seeds of the white-flesh Chinese Cling, and because they are promising varieties for use as parents in breeding work.

Hiley, a probable seedling of Belle, originated with Eugene Hiley, also of Marshallville, Ga., in 1886. Today the Hiley variety ranks second to Elberta as the leading peach of the Southeastern States. It has demonstrated its value as a possible parent in peach improvement because of its high quality and its ability to produce fruits in those southern latitudes where warm winters may be a factor in delaying spring growth and blossoming (fig. 8).

One of the most important varieties that became prominent in the period 1900–1920 is J. H. Hale. This variety was discovered by J. H. Hale as a single tree in a lot of Early Rivers peaches shipped to him by David Baird, of Manalapan, N. J., and planted on his farm at South Glastonbury, Conn. Buds from this tree were taken later to Hale's farm at Fort Valley, Ga. Here the variety also showed great promise as a commercial peach, and it was introduced by Hale through the W. P. Stark Nursery in 1912. By 1925 it ranked fourth

among the freestone varieties grown for fresh fruit in the United States. Present opinions differ as to its value as a commercial variety. It has most of the essential fruit characters of a good commercial peach, but the trees are somewhat dwarfish on some sites and locations, not particularly hardy in wood and bud, and not highly productive. The flowers are pollen-sterile, a serious fault that affects productivity when the variety is planted in solid blocks By and large, the variety

Figure 8.—In southern peach-growing latitudes and in regions with warm winters some varieties are much slower than others in coming out of the rest period after mild winters. On the left is a row of Hiley in full bloom, and on the right a row of Early Rose still dormant. Photographed at Marshallville, Ga., April 12, 1932, a year of marked prolonged dormancy for this region. This is about 5 weeks later than average full bloom.

is not as widely adapted nor as productive as one of its probable parents, the Elberta, and it has not displaced that variety from the position of America's no. 1 commercial peach. However, certain characteristics of the J. H. Hale make it of particular interest to the peach breeder and cytologist. Some genetic features of this variety are discussed later in this article.

Hale introduced another variety, the Early Rose, which proved its commercial importance as an early shipping peach for the Southern States. This soft-flesh cling of fair quality and good color was discovered as a chance seedling growing at Fort Valley, Ga., by John H. Baird, of the Hale farm.

Controlled crossing has been carried on by J. E. Markham, of Xenia, Ill., who, beginning in 1925, developed and introduced to the trade Vivid Globe (Yellow Globe × J. H. Hale), Canadian Queen

(Canadian Banner × Early Elberta), Markberta (Halberta × Canadian Queen), Markham Cling (Golden Cling × Jap Cling), Mark Late (Canadian Queen × Markberta), Globe Haven (South Haven × Vivid Globe), Markham Jewel (Imperial Elberta × Canadian Queen), and Halberta (J. H. Hale × yellow seedling). Most of these varieties have not been widely tested.

Private breeders played a very important part in the work of selecting peach varieties of promise not only from a commercial standpoint but also from that of further improvement of the peach by systematic breeding. Space does not permit listing the many individuals who have been constantly on the watch for the appearance of superior sorts originating as chance seedlings and who subjected the seedlings to careful test. The names of many of these men are given in table 1, together with the description of the varieties they introduced.

Peach Breeding at Public Institutions in the United States

Breeding work with peaches was started at the New York (State) Agricultural Experiment Station at Geneva, N. Y., in 1895, when open-pollinated seeds of the Elberta were planted. No crosses were made until 1910. Work was also begun at the Iowa Agricultural Experiment Station in 1905, when the late S. A. Beach planted some selfed seeds of the Chili in an attempt to develop hardy varieties that would prove resistant to cold. Crandall, at the Illinois station, began work on the development of new varieties about 1907. At the same time work was started at the California station on the development of peach varieties that would be satisfactory for growing in the warm climate of southern California. By 1914 several States had provided funds for peach breeding at a number of State institutions. Peach-breeding studies were begun at the New Jersey station in 1914. The present peach-breeding work in Michigan started at the South Haven Horticultural Experiment Station in 1924. The United States Department of Agriculture began cooperation in peach breeding with this State in 1919 and later cooperated in the work in California. By 1930 there was considerable interest in developing new varieties of peaches by systematic breeding, and variety improvement work has recently been started in a number of other States.

The first promising varieties that resulted from this early station work for replacement of unsatisfactory kinds were introduced in 1925 by the New Jersey station and also by the Horticultural Experiment Station at Vineland, Ontario, Canada. A list of new varieties introduced as a result of systematic breeding and selection work by State and Federal agencies and by the Ontario station for the period 1900–36 is given in table 2.

Work is now being carried on at the various State experiment stations to meet special requirements of the peach industry in the several States. Following table 2 is a summary of the crosses being made and the progeny obtained, beginning with States in which the work has been in progress for the longest time.

TABLE 2.—*Peach varieties developed and introduced by public institutions*

State or Province	Variety introduced	Parentage	Breeder	When crossed	Year named and introduced
California	Babcock	Strawberry × Peento	Citrus Experiment Station, E. B. Babcock and C. O. Smith	1907	1933
Iowa	Polly	Chili (selfed ½ open pollinated)	Iowa Agricultural Experiment Station	1915	1932
Michigan	Halehaven	J. H. Hale × South Haven	South Haven Horticultural Experiment Station	1924	1932
New Jersey	Ambergem	Belle (selfed)	New Jersey Agricultural Experiment Station	1914	1934
	Cumberland	Belle × Greensboro	do	1914	1925
	Buttercup	Lola × Arp	do	1916	1925
	Delicious	Belle × Greensboro	do	1914	1925
	Eclipse	Belle (selfed)	do	1914	1925
	Goldfinch	Slappey × Admiral Dewey	do	1916	1926
	Golden Jubilee	Elberta × Greensboro (open pollinated hybrid)	do	1914	1925
	Marigold	Lola × Arp	do	1916	1925
	Massasoit	Slappey × Admiral Dewey	do	1916	1925
	Meteor	Belle (selfed)	do	1914	1925
	Oriole	Slappey × Admiral Dewey	do	1916	1925
	Pioneer	Belle × Greensboro	do	1915	1925
	Primrose	Belle × Elberta	New Jersey Agricultural Experiment Station	1915	1925
	Radiance	Belle × Greensboro	do	1914	1925
	Rosebud	Carman × Slappey	do	1916	1925
	Sunbeam	Slappey × Admiral Dewey	do	1916	1925
	White Hale	J. H. Hale × Belle or Ray			
	Garden State	Seedling nectarine (self pollinated)	New Jersey Agricultural Experiment Station		
U. S. Department of Agriculture	Maxine	No. 1 Early seedling × Lemon Free	W. F. Wight	1919	1935
	Leeton	Leader (open pollinated)	do	1924	1935
	Stanford	Hauss × Phillips	do	1924	1935
	Ellis	Phillips × Linden	do	1924	1935
Ontario, Canada	Vaughan	Leamington (selfed)	Ontario Horticultural Experiment Station	1913	1925
	Vedette	Elberta (open pollinated)	do	1915	1925
	Veteran	Vaughan × Early Elberta	do	1919	1928
	Valiant	Elberta (open pollinated)	do	1917	1925
	Vimy	Elberta × Arp	do	1916	1925
	Viceroy	Vaughan × Early Elberta	do	1919	1930

New York

To date 65 varieties, 8 seedlings, and 5 P. I.[3] numbers have been used in breeding work at the Agricultural Experiment Station at Geneva. Champion was used 8 times, Crosby 8, Elberta 27, Greensboro 13, Chili 11, Hunter (nectarine) 19, J. H. Hale 11, Krummel 8, Livingston 12, Rivers Orange (nectarine) 10, Rochester 10, South Haven 10, Sure Crop (nectarine) 31, and Veteran 9. There were in all 333 crosses, 24 selfs, and 13 open pollinations. Of the 400 seed-

[3] Trees imported by the Division of Foreign Plant Introduction as well as seedlings grown from seeds brought in are distributed for testing under numbers preceded by the initials P. I.

lings set in the orchard, 307 have originated from crosses made since 1922. Many of the seedlings are just beginning to fruit, and therefore their full history is unknown.

New Jersey

From the work started in 1914, 20 new varieties had been introduced up to the spring of 1936. In addition to these there are 17 unnamed but specially selected peach seedlings showing considerable promise that are now being grown in State-wide commercial tests During the period 1923 to 1936, 6,257 seedlings had been obtained by crossing, selfing, and open-pollinating varieties of peach and nectarine possessing desirable characteristics. Of this number 1,064 have been retained for further study. Approximately two-thirds of this number are of J. H. Hale parentage.

Iowa

One of the objectives of the breeding work at the Iowa Agricultural Experiment Station is to test the feasibility of making interspecific crosses with stone fruits. About 100 potted trees grown in the greenhouse are being utilized in this work. Varieties of *Amygdalus persica*, including nectarines of *A. davidiana* (Carr.) Zabel as well as hybrids between these two species, are being grown. From the crosses made, approximately 75 promising seedlings are now being studied in the field. These include Chili (fourth generation) open-pollinated, Chili (third generation), Bailey × *A. davidiana*, J. H. Hale × *A. davidiana*, and Chili (third generation) × *A. davidiana*.

Illinois

Of the first series of crosses made by Crandall at the Illinois station all have been discarded except Illinois 146, 148, and 101. These are being propagated for further testing under semicommercial conditions. The quality of all three of these is high, but they probably are somewhat lacking in the firmness of flesh that a commercial peach must possess.

Michigan

From the peach-breeding work begun at the Michigan station in 1924, one promising commercial variety, Hale Haven, a cross of J. H. Hale × South Haven, was introduced in 1932. This is a large yellow freestone maturing 17 days before Elberta and about the same time as South Haven. It is considered to be an improvement over the latter variety because of its higher color, thicker skin, and perfect freestone condition. The number of seedlings being grown at the present time from the crosses made during the period 1924–36 is 2,076. During the period 1924–30, 700 seedlings were obtained from crosses of J. H. Hale with a number of commercial varieties important in Michigan, such as Banner, Kalamazoo, Elberta, South Haven, and New Prolific. Of this list only 15 had superior horticultural value.

Work is now under way in an attempt to develop some clingstone varieties of canning types suitable for Michigan conditions. At the present time there are under observation 359 seedlings from crosses where one parent is freestone and the other cling, or where both parents are cling.

California

The work on peach breeding at the California Agricultural Experiment Station at Davis has been confined in recent years (1930–36) largely to developing a satisfactory type of nectarine for canning. A large number of seedlings are now being grown on the station grounds from about 1,310 crosses of nectarine × nectarine and nectarine × peach. Among the varieties of nectarines used as seed and pollen parents are Stanwick, Ansenne, Diamond Jubilee, Sure Crop, Quetta, Boston, Dixie, New Boy, Goldmine, and Lippiatt. Peach varieties used either as seed or pollen parents in crosses with these nectarine varieties are Lovell, Muir, Late Champion, Red Cling, Elberta, Late Crawford, J. H. Hale, Fay Elberta, and Rochester. In addition there is a very excellent collection of over 300 named and P. I. numbered varieties of peach and nectarine as a source of breeding material.

Breeding work with peaches was begun in 1907 at the University of California Citrus Experiment Station, Riverside, to develop varieties for growing in southern California. In this section many of the older varieties of cling and freestone types do not start growth sufficiently early in the spring to secure normal development, and shedding of blossom buds is common following warm winters. The Babcock peach, which was introduced in 1933 by G. P. Weldon, of the Chaffee Junior College, and by the University of California, was the result of the early work started by E. B. Babcock and C. O. Smith and continued by J. W. Lesley. The special value of the Babcock peach lies in its easily broken dormancy. It is an early white freestone of fair size and good quality. In recent years other crosses have been made, using as seed parents various cling and freestone varieties, and pollen from Honey and Peento types and varieties in which dormancy is easily broken. The Babcock is also being used in these crosses. From this work about 12 seedlings have shown promise and are being carried for further testing. Sims pollinated by P. I. 32374 has given a very promising yellow cling. Sims is a variety characterized by a short rest period.

Massachusetts

Breeding work at the Massachusetts station was begun in 1918. The progeny from most of the crosses made in 1925 and 1926, using as female parents varieties that showed considerable hardiness, has been discarded as unsatisfactory for growth under Massachusetts climatic conditions. There are 2,460 seedlings now receiving special study, mostly of a genetic rather than an immediately practical nature. However, a number of promising seedlings have been selected for further testing. In 1931 and 1932 over 2,000 seedlings were obtained in crosses with Belle, Champion, and Gold Drop in studying the problem of linkage between flesh adherence to stone and flesh texture. Some crosses have also been made in a study of the inheritance of bark color.

Virginia

In recent years studies have been made on the progeny of a smooth-skinned Crawford seedling obtained by selfing, when it was crossed with such varieties as J. H. Hale, South Haven, Rochester, Oriole, Golden Jubilee, Elberta, and Gold Drop. The object of the crosses

is to obtain a variety of high quality possessing bud hardiness. Orchard and potted trees are being used. From this work, as well as that previously done with open-pollinated and selfed Elberta, about 15 seedlings of horticultural value have been obtained.

Texas

Breeding studies were begun at the Texas Agricultural Experiment Station, College Station, Tex., in 1935. This work has for its purpose the development of varieties suited to peach-growing districts of Texas where the winter temperatures may not be low enough to give the proper amount of chilling required for best development of varieties that do better in more northern latitudes. Hiley, Pallas, Belle, Early Elberta, Anna, Indian Free, Slappey, and Florida Gem have been used in the crosses.

United States Department of Agriculture

Peach-breeding work in the Department was started in 1919. The early crosses were made at the branch experiment station of the Michigan Agricultural College at South Haven, Mich. Later, crosses were made at the United States Plant Introduction Garden at Chico, Calif. Since 1922 the work has been carried on in the Santa Clara Valley, principally in the experimental orchard at Leland Stanford Junior University, Palo Alto, Calif. Work has recently been undertaken at the United States Horticultural Station at the National Agricultural Research Center, Beltsville, Md., where some 150 varieties are available for study. During the past year 79 separate crosses were made, usually high-quality cold-resistant varieties.

New varieties that have been introduced as a result of the work in California are Leeton, Maxine, Stanford, and Ellis. The Leeton is a selected seedling of Leader grown at Palo Alto from pits imported by Frank Dixon from Leeton, Australia. Maxine is the product of a cross made at South Haven, Mich., between Lemon Free and an unnamed early-ripening seedling of noticeable bud hardiness. The Stanford, a Hauss×Phillips hybrid, is a canning cling peach ripening in season with Phillips. The Ellis, a cross of Phillips×Linden, is also a canning cling type ripening about a week ahead of Stanford. The introduction of these varieties has been based largely upon their behavior under California conditions. The two freestone varieties are worthy of testing under eastern conditions. The Leeton ripens about in season with Triumph and shows promise of being a better early peach than the latter variety. The Maxine is a yellow-flesh variety of high quality, ripening just after Rochester. It has proved to be quite cold-resistant in bud during two recent severe winters (1934–35 and 1935–36) at Beltsville, Md.

A large number of hybrids have been produced since 1922, and these are under test in the experimental orchard at Palo Alto, Calif. Some of the more promising of these hybrids are being tested at other places in California and, in a limited way, in a number of orchards in the eastern United States. Nearly all of the imported freestone varieties produced in this California breeding work are being tested at Beltsville, Md. The seed parents are given in the following list, together with the number of hybrids developed from each parent: Elberta 11,

Hauss 5, Horton Rivers×Chili 8, J. H. Hale 11, Illinois 2, Leader 5, Libbee 8, Lovell 7, Maxine 3, Miller Late 2, Mira 1, Muir 15, Newhall 3, Ontario 4, Paloro 18, Phillips 5, Pratt-Low 10, Salwey 44, Selma 3, St. John 2, Tuskena 14, Uneeda 1, Yellow Free 2, Yellow Transvaal 18.

In addition to the more common commercial varieties, a large number of Department introductions having desirable characteristics and showing considerable promise for breeding have been used. Among these are a Chinese introduction (P. I. 43289) and a Spanish cling (P. I. 43570T2). The varieties listed above as female parents have also been used as pollen parents in a good many reciprocal crosses. Backcrosses and intercrosses have also been made with first-generation hybrids. Studies are being made on the progeny of 234 separate and distinct crosses of named varieties and hybrids. From this group of hybrids a number of promising freestone varieties have been obtained that have characteristics superior to a number of the present commercial varieties. Some are promising canning clings, while others show marked resistance to delayed foliation and are adapted for growing in warmer climates where the present commercial varieties do not produce satisfactory annual crops. Combinations have been made between important commercial varieties subject to delay in foliation and such introduced varieties as Yellow Transvaal and St. Helena, which have less prolonged dormancy, in the hope of transmitting this desirable character to the progeny.

In 1909 Shamel and associates (*29*) noted some striking limb variations in studies of freestone varieties in California, and more recently he has discovered some early- and late-ripening strains among peach varieties. Weldon (*31*) has also reported finding several limb variations in orchards in the same State. It appears that some varieties of peach are less stable than others. While very few color sports of peach have been found to date, it would not be surprising if more should be found when careful search is made.

Peach Breeding in Other Countries

Canada

Since 1914 peach breeding has been carried on at the Ontario Horticultural Experiment Station, Vineland, Ontario, to meet the needs of the market and climatic conditions of southern Canada, especially to secure varieties giving a seasonal succession of ripening. Open-pollinated seedlings have been grown in considerable numbers. Some hybridizing has also been done. Earlier ripening Elberta types with attractive fruit of high quality were sought. In all, 13,106 seedlings were grown during the period 1911–36. Of these, 144 have horticultural value. Six varieties were introduced during the period 1925–30. Two of the most promising, Valiant and Vedette, are Elberta seedlings.

From 1918 to 1922 approximately 2,200 open-pollinated seedlings of Elberta were fruited. A second lot of 1,000 Elberta seedlings bore a marked resemblance to the parent tree in growth characteristics and in fruit. Probably 15 to 20 percent could have been propagated and distributed as Elberta, while approximately 3 percent had white flesh, and 15 percent were semiclings or clings. A fair number were

moderately good, none exceptional, the majority being of Elberta quality or poorer. The variation in season from Elberta was slight, ranging from a week earlier to a week later. Five hundred and fifty open-pollinated seedlings of Lemon Free were almost identical with the parent. Only a very occasional tree bore fruit with even a suggestion of color other than the yellow. Seedlings of New Prolific, Reeves, and Early Crawford were very much like their parents. The fact that open-pollinated seedlings of peach came so true to type when the pits were taken from an orchard in which there were upward of 150 varieties, thus affording every opportunity for natural crossing, suggests that the peach is usually self-pollinated under orchard conditions.

England

Experiments with peaches and nectarines were begun at the John Innes Horticultural Institution, Merton, England, in 1911. The object was to investigate the genetic composition of fruit trees by raising selfed offspring. The varieties used were Royal George, Blood Leaf, and Lord Napier nectarine. The results obtained will be considered later under the discussion of genetic relationships in the peach.

Australia

The work on production of improved varieties of dessert peaches in New South Wales is located at Hawkesbury Agricultural College, Richmond, while that on improved varieties of canning peaches is at the Yanco Experiment Farm, Yanco. Breeding at the Yanco Farm with peaches was begun in 1928. One of the principal objectives was the development of better varieties for canning that would possess high quality, large size, good yield, and freedom from red around the pit. There is a need for early canning varieties to come in immediately after the late apricots are harvested. Table freestone types are also sought in New South Wales, though not specifically in the breeding program at Yanco. The following varieties have been used in crosses as sources of open-pollinated seeds: Golden Queen, Leader, Paloro, Pullars, Sims, Tuskena, Goodman Choice, Locksley Perfection, and Phillips (Victorian strain). Of these the greatest promise as parents has been shown by Golden Queen, Phillips, Tuskena, and Sims (Victorian). Goodman Choice has desirable habits, and Pullars excels in yield but is red around the pit. Leader, a freestone, is one of the best parents. Dessert types that are being planted for orchard trial are Phillips × Triumph, Tuskena × Leader, and La France × Elberta.

At the Hawkesbury Agricultural College, seedlings of Goldmine (nectarine) × Triumph (peach), Blackburn × Triumph, and Elberta × Wiggins have produced fruit of some promise as freestone dessert peaches. With nectarines, work is under way to improve on the standard variety Goldmine. The varieties used as pollen parents are Mrs. Chisholm, W. C. Frip, and Irrewarra.

Morocco

A fruit and vegetable experimental laboratory was established in 1933 for the study of horticultural genetics. Its activities extend to the six experiment stations of the Lacarelle group, distributed in the

different fruit-producing regions of Morocco, as well as to the official experimental gardens of the protectorate. The peach-breeding work has a definite objective, the production of new varieties of high quality adapted to local climatic and soil conditions, as well as stocks resistant to certain diseases, such as gummosis. The work to date has been concerned principally with the study of the hereditary characters of varieties that would appear to be the best parents. A number of hybrids have been produced and are under test. Four forms of the Atlas peach are being used as stocks.

Some Objectives in Improvement of Peach Varieties by Breeding

In surveying the long list of peach varieties available for planting, many are found with very desirable characteristics but for one reason or another not entirely satisfactory from the standpoint of the commercial grower or the home fruit gardener. The fault is often determined by the fruit-growing region in which the particular variety is grown. In one region it may be lack of resistance to winter cold, in another it may be unproductiveness; in still another a peach may prove to be a good bearer with satisfactory cold resistance but lack fruit size and quality. If suitability for canning is the principal requirement in a section, a variety must be judged entirely from this standpoint. Varieties poorly suited for one region or purpose may be entirely suitable for other conditions.

In this article the Elberta has been mentioned as our most important commercial variety, but it lacks some desirable characteristics. It is adapted to a wide range of soil and climatic conditions and is an excellent shipping peach, but it does not have the high fruit quality nor the desired degree of resistance of the tree and blossom buds to low winter temperatures. Where the characteristics of this variety have been combined by breeding with those of a variety more hardy in bud, the results have been promising. A few varieties have been obtained that are of higher quality and more cold resistant in bud than Elberta, but they are not so widely adapted to the fruit-growing regions of this country. Seedlings of the Elberta have been found that ripen ahead of the parent and have fruit of higher quality and more attractive in appearance. So far, when all characteristics are considered, a peach truly better than Elberta has not been found; but if by proper combination of characters a superior variety that is as widely adapted can be produced, it will be a major contribution to American fruit culture. To secure a hardy commercial variety for the colder peach-growing sections of the United States is another most important objective in fruit improvement.

It has long been known that varieties of the so-called Crawford type are of very high quality but not especially productive, and very tender in bud. Varieties of this type have passed out of commercial production because they possessed these unprofitable characters. Attempts should be made to introduce Crawford-type fruit quality or its equal into other varieties, or to combine the hardiness and productive qualities of other varieties with those of the Crawford type. Progress has been made in this direction by using St. John, a Crawford

type of high quality but not particularly strong in tree character and cold resistance in bud, in crosses with Admiral Dewey, an old variety that is particularly hardy in bud, with small, fuzzy, unattractive fruits. A very promising hybrid has been thus developed in the breeding work of the Department of Agriculture.

The J. H. Hale variety has many outstanding fruit characteristics, but it is lacking in vigor of tree, hardiness, and productivity. A cross of J. H. Hale × South Haven at the Michigan Agricultural Experiment Station has resulted in a hybrid showing decided improvement over the South Haven variety. Considerable breeding is under way, using the J. H. Hale variety as a parent. Accomplishments to date, while not entirely satisfactory, give promise for the future.

The raw material represented by varieties of peach in this country needs further reworking through breeding methods in order to obtain the desired combination of characters. In this material there are still many important characters lacking that may be found in varieties now growing in other parts of the world. The need of continuing to import material is apparent. An example is the quest for a variety that is not subject to delayed foliation. In climates with warmer winters than those of the fruit regions of this country, varieties are to be found adapted to such conditions. Such varieties should be introduced into this country for combination with our own. Progress has been made in California in recent years on this aspect of breeding work by the Department of Agriculture. Varieties of the peach of the St. Helena and Transvaal types, introduced respectively from the Island of St. Helena and from South Africa and crossed with our native varieties, have given results that would indicate that the problem of delayed foliation can be overcome at least to some extent through breeding.

There is need for more knowledge about the heritable characteristics of rootstocks for peaches. It has been observed that some varieties of a particular parentage are more susceptible than others to cold injury or to root disease. It is important to know which seedlings may be used as stocks to insure longevity, productiveness, and disease resistance. Work is now under way in the Department of Agriculture to determine the merits of seedlings of known varieties of peach and plum suitable for understocks (fig. 9).

As already indicated, methods must be devised whereby the seeds of early-ripening varieties of stone fruits can be made to germinate after crosses have been made.

Another important objective in stone-fruit breeding work is the development of superior varieties for canning and for drying. In California at the present time varieties of apricots suitable for canning are very much sought for. Varieties of peaches of the canning cling type that have been used for a number of years are not entirely satisfactory because of one weakness or another. Some otherwise satisfactory varieties develop red color in the flesh, especially about the pit, which renders them undesirable for canning. Pit splitting and gumming are other faults. Some of the canning varieties used at the present time are susceptible to mildew through the inheritance of glandlessness. Good types lacking such objectionable characteristics are needed for canning.

The method of approach to the problem of developing better varieties will involve basic studies in the inheritance and transmission of characters. An important part of the work, therefore, will be growing and studying progenies to determine the transmission of desirable as well as undesirable characteristics.

Very little work has been done from the standpoint of securing desirable characteristics through induced mutations. Polyploidy, or increase in the number of chromosomes, which has proved of special interest with other crops, has received little attention from workers in

Figure 9.—Peach rootstock effects. Early Hiley variety, fourth year in the orchard. The row on the right is on plum (*Prunus hortulana*), and the one on the left is on the widely used Tennessee "natural" peach stock. The dwarfing influence on the *hortulana* stock is apparent.

stone-fruit breeding. Some work has been done at the New York Agricultural Experiment Station at Geneva in an attempt to induce polyploidy in stone fruits through the selection of large pollen grains. This method has not yet yielded satisfactory results, but the studies need to be continued, with many other attacks on the general problem. No results have been obtained so far in attempts to cause mutations through heat treatments, a method that seems promising in corn breeding.

Some Genetic Facts Established in Peach Breeding [4]

In a collection of 100 or more peach varieties selected at random, the casual observer of the trees might think that they are all one variety. Among peach varieties in general there are no very marked differences in general tree characters. There are, however, distinct differences in size, shape, and color of leaves, in time of blossoming, in color and size of flower, in time of ripening, and in fruit characters. Genetic studies

[4] This section is written primarily for students and others technically interested in breeding or genetics

show these characters to be inherited, and in hybridization many of them appear in the normal Mendelian ratios. Cytological studies to date have not revealed how the factors governing these characters are linked, nor where they are located on the chromosomes, nor what the behavior is in the reduction division of the sex cells.

Connors (*4*, *6*, *7*), of New Jersey, was one of the first workers in this country to investigate some of the genetic relationships in peaches. He made crosses between some of the important commercial varieties in an attempt to gather information on inheritance of characters.

Inheritance of Flesh Characters

Flesh color.—The parents used by Connors in one series of crosses were Elberta and Early Crawford as yellow-flesh varieties, and Belle and Greensboro as white-flesh varieties. Early Crawford has small blossoms, Elberta medium, and Greensboro large. All are freestone except Greensboro, which is a soft semicling. An analysis of the progeny in the F_1 generation showed some interesting facts. All of the varieties used in the crosses were of unknown parentage, having originated as chance seedlings. Belle, a white, and Elberta, a yellow, are supposed to be F_1 descendants of Chinese Cling, with the pollen parent unknown. Greensboro behaved as a pure white in crosses, but when selfed no progeny was obtained because of the failure of the seeds to grow. St. John (yellow) × Early Wheeler (white) gave all white in the F_1, and St. John × Greensboro likewise gave all white F_1 seedlings. White flesh is dominant over yellow flesh. Crosses or self-pollinations of homozygous white-flesh varieties have yielded all white-flesh seedlings. Heterozygous whites have yielded three whites to one yellow. Yellows have given all yellow.

This work makes the supposed parentage of Elberta somewhat open to question. Elberta is a seedling of Chinese Cling, and the pollen parent is thought to be some variety like Early Crawford. If Chinese Cling were pure white, as might be suspected from its early history, then in a cross with a yellow variety the first generation seedlings should all be white. However, Elberta as the F_1 in this probable cross is yellow, while Belle, a seedling of the same variety (Chinese Cling) is white. The Chinese Cling parent of Elberta may not have been a pure white. The work at Vineland, Ontario, Canada, reported by Palmer (*26*), confirms that of Connors in showing that when a homozygous white-flesh peach has been used as one of the parents, all of the progeny will have white flesh. Yellow flesh behaved as a pure recessive. It is perhaps more significant in considering the parentage of Elberta that from 2,200 open-pollinated and selfed seedlings of that variety, there has been none with fruit resembling Early Crawford, the supposed pollen parent. Palmer has ventured the opinion that Elberta is a natural selfed seedling of Chinese Cling, a recessive yellow breeding true for that color.

Texture of flesh.—In the work of Connors, Elberta self-pollinated seedlings showed a high percentage of firm fruit. Wherever Elberta was used as a parent the result was a high percentage of firm-flesh seedlings. Belle × Early Crawford gave a relatively high percentage of firm-flesh seedlings. Soft flesh appears to be dominant over non-melting flesh. The character for producing the tough flesh so desirable

for commercial canning is present in Belle, Carman, and Early Crawford. Seedlings of these varieties, however, show red coloring of the flesh about the stone, an undesirable character from a canning standpoint.

Adhesion of flesh to stone.—Connors noted that freestone appears to be dominant over clingstone. In crosses between freestone varieties the progeny has been about two freestones to one cling or semicling. There are some varieties that are classed as semicling in which the adhesion of flesh to stone is not very great. In some of these groups such as Greensboro and Carman, the fruits in some seasons may be nearly free. Frequently, if the fruits are allowed to remain on the tree until well ripened, the flesh will almost completely separate from the stone. The true clingstone type of peach is that represented by varieties like White Heath and Red Bird, and the canning cling by types like Phillips and Paloro. Freestones crossed with freestones always gave a high percentage of freestones, the degree depending on the variety. Belle and Elberta carry a factor for adhesion of flesh to stone of about 33 percent. When freestones are crossed with clingstones a higher proportion of freestones than clingstones is obtained.

Inheritance of Other Characters

Foliar glands or nectaries.—The foliar nectaries of the peach are of interest because it has been shown that glandless varieties are more susceptible to some leaf diseases, particularly mildew, than varieties with glands. Some commercial canning cling varieties now grown in California, such as Paloro and Hauss, are glandless. These are quite subject to mildew in some seasons and in some locations. Rivers (*27*) reports that in crossing varieties having reniform glands with glandless varieties, he obtained an intermediate type, which was round or globose. Connors, in crossing some of our common American varieties, such as Belle, Carman, Elberta, and Greensboro, which are reniform, obtained seedlings all of which were reniform. When these varieties were crossed with varieties with globose leaf glands, the progeny was about 50–50 reniform and glandless. No glandless varieties were selfed, but Bailey and French (*2*) report all the progeny of a selfed glandless seedling were glandless. The F_1 hybrids of a cross between reniform and glandless varieties all have glands that are globose (fig. 10). The character is apparently incompletely dominant.

Tree habit.—In crosses at the New Jersey station between Greensboro, spreading type, and Early Crawford, upright type, the seedlings were all intermediate, none being the same as either parent. Seedlings of Early Crawford, self-pollinated, were all upright. Seedlings of Lola and Carman, which are spreading, were all spreading. The progeny from selfed Elberta gave ratios of 1 upright : 2 intermediate : 1 spreading. No dwarfs have appeared among the progeny of these varieties.

Size of blossoms.—With blossoms the blending type of inheritance is usually shown, with sometimes a slight apparent dominance of the small-blossom type. In all cases studied by Connors, the large blossoms and small blossoms were homozygous. Large crossed with small gave all medium, and the medium split up in a ratio of 1 : 2 : 1 in the F_2 generation. Large blossoms appear to be dominant in varieties

bearing them, while varieties with small blossoms give small blossoms in selfing. In crosses of large-petal types with small-petal types all the seedlings had medium-size blossoms. This appears to be a case of incomplete dominance.

Blooming date.—The majority of seedlings bloomed at practically the same season as the parents, but a few individuals bloomed earlier or later. Elberta and Belle, self-pollinated, gave some seedlings that commenced blooming as much as a week after the parents. Slappey is a late bloomer, and all of its progeny were late.

Ripening date.—The hybrids usually ripened about midway between the parents, and it is rarely the case that a seedling ripens

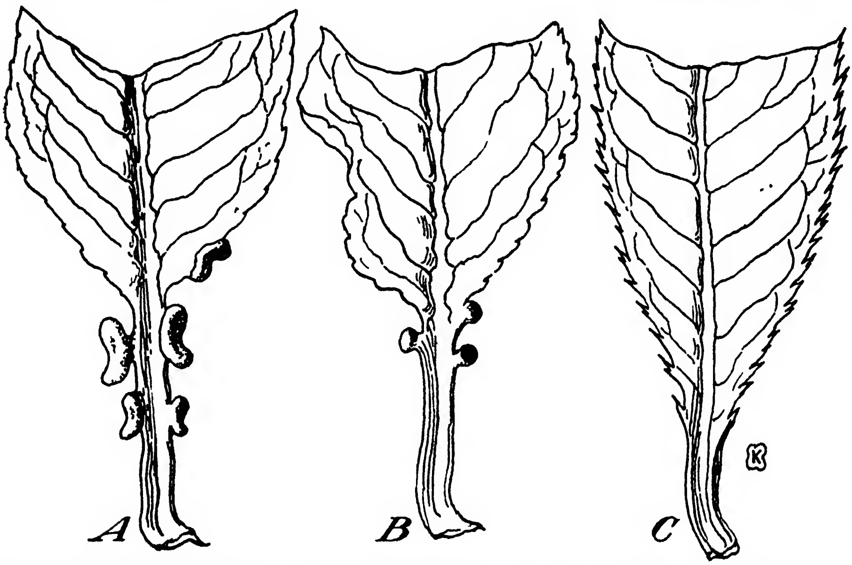

Figure 10.—Types of foliar nectaries in the peach and the nectarine: *A*, Reniform or kidney-shaped glands of Elberta peach; *B*, globose glands of Fitzgerald peach; *C*, eglandular leaf of Lippiatts nectarine.

earlier than the early parent or later than the late parent. The deduction is that the best chance to secure a new individual ripening its fruit at a certain date would be by crossing two varieties the mean of whose ripening dates would fall at the desired time. No marked differences in ripening dates were observed. The majority of the seedlings of the varieties used ripened about in season with the parents, with some slightly earlier and some later than either parent.

Size of fruit.—Parents with small-size fruit are to be avoided. Belle transmitted its character for good fruit size. Elberta seedlings are practically all large-fruited.

Beginning in 1921, Connors used the J. H. Hale variety in a number of crosses. During the period 1923–28, 42 crosses were made with this variety. Blake and Connors (*4*), reporting on the results of these crosses, state that the collection of characters in the J. H. Hale variety was as a group recessive to the characters in varieties such as Chili, Iron Mountain, Chinese Blood, and varieties with nonmelting type

of flesh. In the case of J. H. Hale × Chili the progeny of the cross so closely resembled Chili in every way that it was impossible to distinguish many of them from the pollen parent. In summarizing the evidence of inheritance of characteristics in the progeny of these J. H. Hale crosses, Blake and Connors drew the following conclusions: (1) Red flesh color about the pits is apparently dominant over absence of red at the pit; (2) watery melting flesh texture is apparently dominant over firm-melting flesh texture; (3) nonmelting flesh is recessive to both watery melting and firm-melting flesh texture; (4) blood red flesh was dominant over the absence of red; (5) heavy pubescence is apparently dominant over short or light pubescence; (6) oval-conic, oval-oblong, and round-pointed forms in Chili, Iron Mountain, Chinese Blood, Japan Dwarf Blood, and others were dominant over round; (7) full-dwarf and semidwarf growth habit was recessive to standard tree size; (8) early blooming, characteristic of *Amygdalus kansuensis* (Rehd.) Skeels, was dominant over the late blooming of J. H. Hale; (9) vigorous sucker development from the trunk and main branches characteristic of *A. kansuensis* was dominant over the slight sucker development of J. H. Hale.

Characters Transmitted by Certain Varieties

Elberta transmits large fruit size, yellow color, and firmness of flesh, freestone character, an extended period of ripening, and a slight tendency to sterility. The self-pollinated seedlings show better quality than that of the variety itself.

Belle is a heterozygous white and is able to transmit white and yellow flesh, a fair degree of firmness of flesh, a fair degree of freestone condition, variability in period of ripening and blooming, and a tendency to sterility.

Early Crawford transmits small fruit size, yellow flesh, a good degree of firm or tough flesh, a fairly high degree of freestone character, tender pubescent skin, and rather high acidity.

Greensboro transmits white flesh, good fruit size and color, hardiness in bud, softness of flesh, and a clingstone character.

Slappey transmits small fruit size, dry, mealy, yellow flesh, lateness of blooming, and nonadhesion of pulp.

Lola transmits small size, tendency to clingstone condition, and tough flesh.

In tree habit the white-flesh varieties are more vigorous in tree growth than yellow-flesh sorts.

Further genetic studies on the inheritance of characters in the peach may be helpful in tracing the origin of the aforementioned groups or races of peaches. This should be possible if prototypes of our present-day varieties could be located, such as the large-petaled, white-fleshed peaches of China, and the small and medium-petaled, yellow-fleshed types found among varieties more common in western Asia and the Mediterranean countries, and among the varieties now commonly grown in this country.

Genetic Studies in England

Work at the John Innes Horticultural Institution in England with the peach Royal George, having small flowers and small, eglandular, serrate leaves, when selfed gave a progeny of seedlings with small

flowers and eglandular, serrate-margined leaves. Royal George and its progeny proved to be susceptible to mildew.

The Purple Leaf variety of peach (Blood Leaf) with large flowers, purple leaves, reniform glands, shallow margin, finely serrate, when selfed gave a small number of progeny, all having large flowers, purple leaves, reniform glands, and leaf margin similar to type.

Selfed nectarine (Lord Napier variety) with large flowers, large leaves, reniform glands, and shallow crenate margin gave seedlings with flowers and leaves similar to the parent. A few of the leaves were almost serrate.

Two seedlings raised from a cross of Purple Leaf peach × Lord Napier nectarine had purple leaves, but the pigment was less intense than in the Purple Leaf parent or its selfed derivatives. This suggests that the purple pigment in the peach behaves as a dominant, but the reduction in the amount of pigment suggests a modifying factor.

Correlations

Hedrick (*17*) has pointed out a correlation between color of the inside of the calyx cup and the color of flesh of the fruit. When the calyx cup is greenish the fruit will be white, and when the calyx cup is a deep orange the flesh of the fruit will be yellow. An intermediate type is suggested by Connors in which the calyx cup is yellowish buff, and following this the color of the flesh will be white, but the tree carries a character for yellow flesh. This is true in the case of Belle.

Another correlation, according to Connors, is that between leaves and the color of the flesh. When the midrib and the veins of the leaves of a variety have a yellowish cast the fruit is yellow, but if the midrib or veins are pale green or whitish the fruit will be white.

Pollen Sterility

Most varieties of peaches are self-fruitful. Occasionally failure to produce crops may be due to pollen sterility, which is exhibited in a few commercial varieties, such as J. H. Hale, Halberta, Candoka, Mikado, and Chinese Cling.

Connors in 1921–22 examined over 330 seedlings in the fruit-breeding plots. J. H. Hale was the only variety that did not produce pollen, and about 50 percent of open-pollinated seedlings of this variety were pollen-sterile individuals. Progeny of some crosses with J. H Hale have also shown about 50 percent of sterile individuals, while in other crosses with this variety the progeny all produced pollen. It is suggested that this type of sterility is recessive to the fully fertile flower form. The failure of pollen-grain development in J. H. Hale has been found to be due to degeneration in the microspores some time previous to blossoming. Apparently there are strains of this variety that produce pollen and are self-fruitful, but whether these have arisen as somatic variations or have distinct ancestry is unknown.

Among seedling peach progenies examined the percentages showing pollen sterility were: Belle selfed 21 percent, Belle × Elberta 17, Elberta × Belle 14, Elberta selfed 13, Elberta × Early Crawford 7, Elberta × Greensboro 5, and Belle × Greensboro 4 percent.

Chromosome Numbers in Peach Varieties

The basic chromosome number in the sex cells in the genus *Prunus* is 8. The varieties of peach examined cytologically show the diploid (2*n*) number of chromosomes to be 16. So far as known, no triploid or tetraploid types have been discovered. If these have occurred in the past they have apparently not been propagated or were discarded in the search for new varieties. The fruit characteristics of the J. H. Hale variety might suggest a tetraploid condition, but insofar as is known they are not associated with tetraploidy.

The peach is rather a stable entity. No irregularities in chromosome behavior have been reported. Apparently reduction to the haploid number in the formation of the sex cells prior to fertilization and fruit development proceeds in a normal manner. Likewise in somatic cell divisions no conspicuous irregularities have been reported in chromosome behavior, and few varieties have been propagated as true somatic mutations.

The problem of self-unfruitfulness, which is very important in the case of other stone fruits and of apples, and which has stimulated considerable cytological investigation with these fruits, is relatively unimportant in the peach.

Nearly all of our commercial varieties are self-fruitful, that is, they set fruit with their own pollen. In a few instances varieties are self-unfruitful because of pollen sterility.

Our present-day varieties are largely considered to be chance seedlings, and many of them may have arisen as self-pollinated progeny of various types. Some doubtless are the result of natural hybridization. It is a fact, however, that many of these varieties are homozygous for the genes controlling several of the characters studied.

APPENDIX (PEACH)

TABLE 3.—*Locations of peach-breeding work and names of workers in the United States and Canada*

State or Province, institution, and location	Year work was begun	Early workers	Workers actively engaged at present
California:			
Agricultural Experiment Station, Davis.	1925	----------	W. A. Tufts, G. A. Philp.
Agricultural Experiment Station, Riverside.	1907	E. B. Babcock, C. O. Smith, H. B. Frost.	J. W. Lesley.
Chaffee Junior College, Ontario	----	----------	George P. Weldon.
U. S. Department of Agriculture, Palo Alto.	1922	----------	W. F. Wight, L. A. Thompson.
Illinois:			
Agricultural Experiment Station, Urbana.	1907	C. S. Crandall	J. C. Blair, M. W. Dorsey, J. C. Whitmire.
Iowa:			
Agricultural Experiment Station, Ames.	1900	S. A. Beach	T. J. Maney.
Maryland:			
U. S. Department of Agriculture, Beltsville.	1931	----------	F. P. Cullinan, J. H. Weinberger.
Agricultural Experiment Station, College Park.	1929	E. C. Auchter, W. L. Kerr.	A. L. Schrader, S. W. Wentworth.
Massachusetts:			
Agricultural Experiment Station, Amherst.	1918	----------	J. S. Bailey.
Michigan:			
Agricultural Experiment Station, South Haven.	1924	----------	Stanley Johnston, V. R. Gardner.

TABLE 3.—*Locations of peach-breeding work and names of workers in the United States and Canada*—Continued

State or Province, institution, and location	Year work was begun	Early workers	Workers actively engaged at present
New York:			
Agricultural Experiment Station, Geneva.	1895	S. A. Beach	U. P. Hedrick, R. Wellington, Olav Einset.
New Jersey:			
Agricultural Experiment Station, New Brunswick.	1914	C. H. Connors	M. A. Blake.
Texas:			
Agricultural Experiment Station, College Station.	1935		S. H. Yarnell.
Virginia:			
Agricultural Experiment Station, Blacksburg.	1925		Fred W. HofMann.
Ontario, Canada:			
Horticultural Experiment Station, Vineland.	1914		E. F. Palmer, G. H. Dickson.

Peach and Nectarine Breeding Material at the United States Horticultural Station at the National Agricultural Research Center, Beltsville, Md.[5]

PEACHES

Admiral Dewey
Admiral Dewey × St. John
Alexander
Alton
Australian Saucer
Babcock
Banner
Barnard
Belle
Beers Smock
Berk Favorite
Best June
Bilyeu
Blood Flesh
Brackett
Briggs Red May
Canadian Queen
Candoka
Captain Ede
Carman
Chili
Chinese Cling
Champion
C. O. Smith
Cumberland
Curry
Delicious
Duke Hale
Early Crawford
Early Elberta
Early Imperial
Early Queen
Early Rose
Early Wheeler (Red Bird)
Eclipse
Elberta
Elberta × Phillips
Engle Mammoth
Eureka
Fairs Beauty
Father's Pride
Fay Elberta
Fitzgerald
Fei
Flaming Gold
Fox
Frances
Gage
George IV
Giant Snowball
Globe
Gold Drop
Gold Finch
Golden Jubilee
Greensboro
Halberta
Halehaven
Hale Early
Hauss × Foster
Heath Cling
Henrietta
Hiley
Hobson
Honey Dew
Hope Farm
Horton River
Hyslop
Illinois
Improved Crawford Late
Indian Blood Cling
Iron Mountain
Japanese Giant Cling
J. H. Hale
John Rivers
July Elberta
July Gold
June Elberta
Kalamazoo
Kathryn
Kette
Krummel
Late Crawford
Leeton
Lemon Cling
Lemon Free
Levy
Libbee
Linworth
Lovell
Loving Cling
Luken Honey
Mammoth Heath Cling
Marigold
Mark
Markham Cling
Marquette
Martha Fern
Mathews
Maxine
Mayflower
Mikado

[5] The variety names in this and the following lists conform so far as practicable to the code of fruit variety nomenclature. However, among them there is a considerable number of introductions from other countries, selected strains of standard varieties tentatively designated, and other names applied temporarily, which cannot be made to conform readily to the code. The publishing of such names in this connection is not to be construed as the acceptance of them by this Department.

Miller Late
Minnie Stanford
Mountain Rose
Muir
Newcomb
Newhall
New Jersey 71
New Jersey 73
New Jersey 87
New Prolific
Niagara
N. J. 12722
Oldmixon Cling
Oldmixon Free
Opulent
P. G. W.
P. I. 36126
P. I. 43137
P. I. 68353
P. I. 101655
P. I. 101663
P. I. 101665
P. I. 101667
P. I. 101668
P. I. 101669
P. I. 101675
P. I. 101676
P. I. 101677
P. I. 101680
P. I. 101681
P. I. 101682
P. I. 101687
P. I. 101688
P. I. 101689
P. I. 43289 × Early Crawford
Pallas
Peacharine
Peak Cling
Phillips
Pickett Favorite
Pioneer
Polly
Pratt Low
Ray
Red Indian
Rio Oso Gem
Roberta
Rochester
Radiance
St. John
Salberta
Salwey
September Mammoth
Shalil (P. I. 63852)
Shippers Late Red
Sims
Slappey
South Haven
Stinson
Strawberry
Stump
Sun Glo
Texan
Triumph
Uneeda
Valiant
Vedette
Veteran
Viceroy
Vivid Globe
White Cling
White Hale
Wilma
Yellow Indian

NECTARINES

Boston
Gold Mine
Gower
Hunter
Lipiatt Late Orange
Quetta
Rivers Orange
Stanwick
Sure Crop

Peach and Nectarine Breeding Material at the California Agricultural Experiment Station, Davis, Calif.

PEACHES

Admiral Dewey
Al
Alexander
Alpha Tuscan
Alton
Amsden
Angel
Annabel
Arp
Australian Saucer
Babcock
Banner
Barbara
Belle
Belle October
Best June
Bitterless Elberta
Bilyeu
Blood
Blood Cling
Blood Free
Blood Leaf Cling
Bokhara
Bolivian Cling
Brackett
Bresquilla
Briggs
Brock Beauty
Buckhorn
Burton's Hale Early seedling
Cameo
Captain Ede
Carman
Carota
Carpenter
Champion
Chiloro
Cumberland
Cotogna di Siena
Crimson Cling
Cuban Nut
Currie Free
Dahling
Day Late Cling
Decker
Dorothy
Duchess of Cornwall
Earliest
Early Charlotte
Early Crawford
Early Elberta
Early Imperial
Early Japanese
Early Rose
Early Wheeler
Elberta
Elberta Cling
Estella
Eureka
Everbearing
Fay Elberta
Fei
Fitzgerald
Florida Gem
Florence
Foster
Frank
Frank seedling
Fredericka
Gaume
George IV
George Late
Gibbon October
Gilla Tardiva di Milano
Gillingham
Globe
Gold Dust
Goodman Choice
Golden Chinese
Golden Jubilee
Golden Sweet Cling
Golden Queen
Greensboro
Grosse Mignonne
Haight Late Free
Hale Cling
Hale Early
Harris
Harris Yellow Cling
Halford No. 1
Halford No. 2
Halford No. 3

Heath Cling
Helen
Hobson
Home Freestone
Honey
Honey Cling
Ideal
Ijam Tuscan
Illinois
Imperial
Japan Dwarf
Jewel
J. H. Hale
J. H. Keith Early May
Johnson
June Elberta
Katie
Klondike
Krummel
Lady Lindsey
Lady Palmerston
La Grange
Late Champion
Late Crawford
Late Elberta
Late Tuscan
Leader
Lemon Cling
Leona
Levy
Libbee
Liberty
Lippiatt
Lovell
Luken Honey
Mammoth Heath
Massasoit
Mary
Mayflower
McDevitt Cling
McKevitt
Miller Late
Ming Tomb
Minnie Stanford
Mississippi
Monte Vista Cling
Morellone
Morris White
Mother
Motions Cling
Mothers Favorite
Mountain Rose
Mowry Strawberry Cling
Muir
Muir Perfection
Munford
National
Newcastle Tuscan
Newhall
New Jersey
Niagara
Nichols
Noble Red
October Beauty
October Indian
Octoberta
Oklahoma Beauty
Oldmixon Cling
Oldmixon Free
Ontario
Opulent
Orange Cling
Oriole
Osprey
Pallas
Paloro
Paragon
Patison
Peak
Peento
Peregrine
Perfection
Phillips
P. I. 24807
P. I. 32374
P. I. 35201
P. I. 36485
P. I. 41395
P. I. 43289
P. I. 43290
P. I. 43291
P. I. 55563
P. I. 55564
P. I. 55813
P. I. 55835
P. I. 61302
Picquet Late
Pinkham
Placer Cling
Pomona
Pratt Low
Prince of Wales
Pullar Cling
Radiant
Raisin Cling
Radiance
Red Bird (synonym of Early Wheeler)
Rio Oso Gem
Rochester
Runyon Orange Cling
Red Muir
Sabichi Winter
St. John
Salwey
Sea Eagle
Sellers
Selma
Shamrock
Shalil seedling
Sharpe
Sherman
Shippers Cling
Sims
Smith
Smith Indian
Sneed
Stearns
Stinson
Strawberry
Summer Heath
Sunbeam
Sullivan
Stump
Suber
Susquehanna
Sutter Creek
Taylor
Tena
Texas
Thurber
Thurmond
Togo
Tosetti Late Free
Triana
Tribbles Cling
Tribbles Free
Tribbles Price
Triumph
Tuscan (synonym of Tuskena)
Tuskena
Up-to-Date
Vainqueur
Van Emmon
Vivid Globe
Victor
Waldo
Walton
Ward Late
Washington
West Late Free
Wilbur
Wiley Cling
Wilma
Winter Freestone
Worth
Yellow Hiley
Yellow Swan

NECTARINES

Advance
Ansenne
Boston
Breck
Cardinal
Davis
Diamond Jubilee
Dixie
Downton
Dryden
Early Newington
Early Rivers
Fisher Yellow
Gaylord
Gold Mine
Gower
Griffith
Hardwiche

Humboldt
J. C. Wees
Kathryn
Lippiatt
Lord Napier
Mexican
Milton
Muir
Nettarino Gilla d'Padova
New Boy
New White
Nigh
Newton
Ozark
P. I. 26503
P. I. 29227
P. I. 30648
P. I. 65973
P. I. 65974
P. I. 65975
P. I. 65976
P. I. 65977
P. I. 65978
P. I. 65979
P. I. 68178
Pineapple
Quetta
Red Cling
Red Roman
Robinson
Smith
Spanish
Spencer
Stanwick
Stanwick Elrudge
Surecrop
Togatch Moneck
Traveller
Victoria
Violet
Wilkinson

Peach and Nectarine Breeding Material at the Georgia Agricultural Experiment Station, Experiment, Ga.

PEACHES

Admiral Dewey
Alton
Annabel
Belle
Babcock
Banner
Best June
Best May
Brackett
Chilow
Chinese Cling
Cumberland
Delicious
Eureka
Early Rose
Eclipse
Elberta
Fertile Hale
Fitzgerald
Florida Gem
Gage Elberta
Georgia Hale
Golden Jubilee
Goldfinch
Halehaven
Hale seedling
Harpole Late Yellow
Honey
Indian Blood
Jewel
J. H. Hale
Kette
Krummel
Lemon Free
Luttichau
Manly
Marigold
Marquette
Mayflower
Mikado
Mountain Rose
New Jersey 46–B
New Prolific
Oriole
Paloro
Paloro No. 2
Picquet Late
Phillips No. 1
Pioneer
Rio Oso Gem
Riverdale
Rochester
September Mammoth
Shipper Big Red
Sims
Slappey
Sunbeam
Sun Glo
Tuskena (Tuscan)
Valiant
Vedette
Veteran
Walton
Weem Hale
White English
Willow Leaf
Wilma
Woodland Cling

NECTARINE

Red Roman

Peach and Nectarine Breeding Material at the New Jersey Agricultural Experiment Station, New Brunswick, N. J.

PEACHES

A–1 on Salwey Seedling (43124)
Admirable Jaune (P. I. 86168)
Admiral Dewey
Agostina (80128)
Aicken Cling (P. I. 88543)
Alberge Jaune (P. I. 101820)
Amarillo Tardio (P. I. 55835)
Amarillo Tardio (P. I. 55836)
Ambergem
Ames 2
Anna
Arp
Augbert
Aurora (P. I 57688)
Australian Saucer
Banner
Barbara
Beauty Belle
Belle de Vitry (P. I. 102515)
Bennetts Perfection
Berks
Best June
Bilmeyer
Bolivian (P. I. 36126)

Brackett
Briggs Early May (synonym of Briggs)
Burbank
Burbank Giant Freestone
Buttercup
Camelliaflore
Candoka
Chairs Choice
Charles Ingouph (P. I. 101825)
Chili
Chinese Blood
Chinese Cling
Clam Shell Elberta
Colora
Columbia
Connett
Crosby
Cumberland
D. B. Ansac (P. I. 88546)
Delicious
D'Italia
Double Pink
Double Red Early
Double White
Duke of York
Dulce
Eagles Beak (P. I. 43289)
Early Crawford
Early Elberta
Early May
Early Rose
Early Wheeler
Eclipse
Elberta
Elberta Dwarf
Engle Monmouth
English Galande
Estella
Eureka
Exquisite
Fertile Hale
F. H. B. (43051)
Fitzgerald
Foster
Fox
Frances
Frank
Fredericka
Gallande (P. I. 66094)
Gemmer
General Lee
George IV
Gold Drop
Golden Elberta Cling
Golden Gem
Golden Heath
Golden Jubilee
Goldfinch
Goodman Choice on Salwey (68354)
Gordon
Goshawk
Greensboro
Grosse Mignonne (P. I. 76357)
Grosse Mignonne (P. I. 91763)
Grosse Mignonne (P. I. 102523)
Halberta
Hale Early
Halehaven
Hann Almond
Hardee
Harpole Late Yellow
Hauss
Heath Cling
Hiley
Hobson
Hope Farm
Ice Cream
Ideal
Illinois
Indiana
Indian Blood Cling
Indian Cling
Iron Mountain
Isquierdo (P. I. 57687)
Japan Dwarf Blood
Japan Golden Giant Cling
Jennie Worthen
J. H. Hale
J. M. Mack
July Elberta
July Gold
June Elberta
Kalamazoo
Kathryn
Katie
Kette
Kihi Kihi (P. I. 88547)
King Solomon
Krummel
Late Champion
Late Crawford
Late Elberta
Leeton
Lees Salwey (P. I. 88548)
Lemon Cling
Lemon Free
Leona
Lizzie
Lippiatt Late Red
Madeleine de Courson (P. I. 66095)
Mamie Ross
Marigold
Marquette
Marriages Late (P. I. 88550)
Massasoit
Maxine
Mayflower
Mexican Honey
Mitchelson (P. I. 88551)
Monkton No. 1 (P. I. 88552)
Monkton No. 2 (P. I. 88553)
Morris White
Motions Cling
Mountain Rose
Muir
Muir Perfection
National
Ohio Late Crawford
Oldmixon Free
Oriole

Pallas
Paloro
Pomona Majorada (P. I. 57689)
Paragon
Prunus davidiana
Peacharine
Peento
Phillips
P. I. 35201
P. I. 36485
P. I. 55564
P. I. 55775
P. I. 55776
P. I. 55885
P. I. 55886
P. I. 55887
P. I. 55888
P. I. 56920
P. I. 61302
P. I. 63850
P. I. 63851
P. I. 63852
P. I. 63853
P. I. 63855
P. I. 74011
P. I. 76202
P. I. 76361
P. I. 88562
P. I. 88561
P. I. 91762
P. I. 92159
Pioneer
Plummer (P. I. 88565)
Polly (Ames 11)
Poppa de Venere (P. I. 102527)
Primrose
Prunus kansuensis
Prunus mira
Pullar Cling
Purple Leaf
Radiance
Ray
Red A
Red B
Red C
Red D
Red Bird (synonym of Early Wheeler)
Reeves
Reina Eleana (P. I. 57690)
Red Magdelaine (P. I. 57691)
Rio Oso Gem
Rochester
Rosebud
Salberta
Salwey
Sant Anna (P. I. 102530)
Sargents
Sellers Orange
Semi-Dwarf Elberta
September Monmouth
Shippers Cling
Shippers Late Red
Slappey
Sleepers Dwarf
Smock
South Haven
Stevens
Stinson
St. John
Strawberry Free
Stump
Sunbeam
Sun Glo
Sungold
Surprise
Tos China (P. I. 77877)
Tos China on Salwey (P. I. 77878)
Tos China on Salwey seedling (P. I. 77876)
Triumph
Tuskena (Tuscan)
Up-to-Date
Valiant
Vanity
Veteran
Vidette
Volaric (P. I. 107783)
Waipawa on Salwey seedling (88556)
Waldo
Watt Early (P. I. 57917)
White Hale
Wilma
Winner
Wm. Kane
Wrights Bountiful (P. I. 88567)
Wrights Late Red (P. I. 88558)
Wrights Midseason (P. I. 88559)
Yellow Greensboro
Zelandia Peach (P. I. 88560)

NECTARINES

Blood Fleshed
Breck
Cardinal
Diamond Jubilee
Flaming Gold
Garden State
G. O. Breeding
Goldmine
Gower
Humbolt
Lippiatt Late Orange
Nectarine Peach (P. I. 88554)
Littles Yellow
Lord Napier
P. I. 65973
P. I. 65974
P. I. 65975
P. I. 65976
P. I. 65977
P. I. 65978
P. I. 65979
Pineapple
Sure Crop
Victoria
Yennman

PLUMS

In the United States, as well as in Europe, the plum has long been recognized as one of the most delicious of fruits, and among the stone fruits it ranks next to the peach in commercial production. Many of the varieties of plums now cultivated in the United States have been introduced from many foreign countries, and when these are added to the native varieties they give plums the largest number and greatest diversity of kinds and species among the stone fruits. The fruits exhibit a wide range of size, flavor, color, and texture. The plants vary from small shrubs with drooping branches to trees of large size with large, upright branches, and some have great beauty as ornamental plants (*3*, *19*, *34*).

The common European plum, known botanically as *Prunus domestica* L., appears to have originated somewhere in southeastern Europe or western Asia, probably in the region around the Caucasus and the Caspian Sea. Although it is called the European plum, De Candolle, who summarized the history of these stone fruits, is very doubtful whether *P. domestica* is indigenous to Europe. According to the earliest writings in which this plum is mentioned, the species dates back some 2,000 years. Another Old World plum species, probably of European or Asiatic origin, is the damson plum, *P. insititia* L. This species seems to antedate *P. domestica*, as is suggested by the finding of damson plum pits in ancient ruins. The ancient writings connect the early cultivation of these plums with the region around Damascus.

It is not known just when European plums were introduced into North America, but probably pits were brought over by the first colonists. It is reported that plums were planted by the Pilgrims in Massachusetts, and importations were made by the French into Canada. These European plums have done remarkably well in the New World, and today they constitute the most important group grown commercially for canning and drying.

The native American plums were doubtless used for food by the Indians long before the white man set foot on the shores of this continent. Reports of early explorers mention the finding of plums growing in abundance. According to the descriptions of the early settlers, these plums were inferior to the domesticas of the Old World in quality, so that the colonists soon began importing varieties from Europe. As a result, European plums soon became predominant in home fruit gardens as well as commercial orchards in the northeastern United States.

Another important species of more recent introduction into North America is the Japanese plum, *P. salicina* Lindl., which was domesticated in Japan and was introduced into the United States about 1870.

The Raw Material of the Plum Breeder

Cultivated varieties of at least 12 species of plums are to be found in American orchards or growing in the wild, but most of the important commercial varieties are confined to 4 of these species. A wealth of types, varieties, and species is available for the fruit breeder.

The best known and most important of these groups are varieties of *Prunus domestica*, the European plums and prunes. Unfortunately

they are not well adapted to regions with hot, dry summers or dry, cold winters. They are at home in the northeastern United States; in sheltered sections along the Great Lakes and in the Intermountain and Pacific Coast States they are at their best, as is evidenced by the extensive production of fresh fruit and dried prunes in this region. The European plums have been under domestication longest, and the

Figure 11.—Types of fruit in the group of *Prunus domestica*: *A*, Reine Claude, a high-quality plum of the Green Gage group; *B*, Bradshaw, formerly an important variety in the Lombard group of reddish plums used for canning and dessert, but being replaced by better varieties produced as a result of hybridization and breeding; *C*, Diamond, a blue plum of the Imperatrice group. The varieties of this group are of medium size, dark blue in color, with a heavy bloom.

fruits are notable for large size and attractive appearance. They vary in color from the green and golden yellow or the Reine Claude (Green Gage) and Yellow Egg groups to the red and dark purple of the

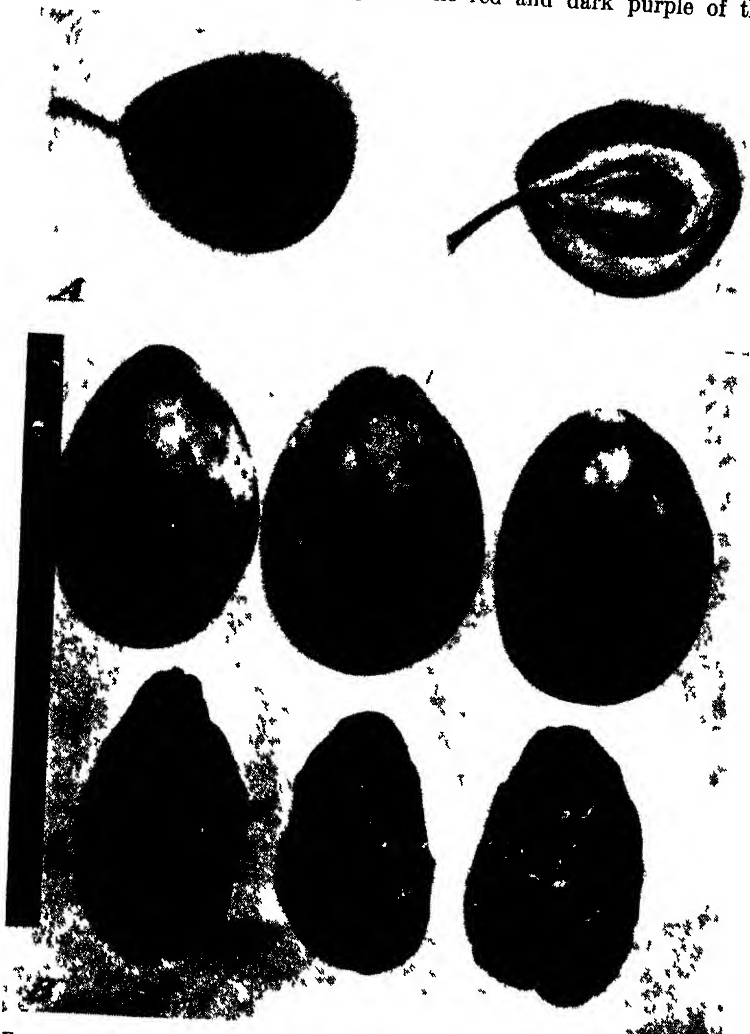

Figure 12—Some of the most important varieties of *Prunus domestica* used for making prunes: *A*, Italian Prune, showing the shape of the fruits in the prune group, *B*, some varieties that produce large prunes when dried

Lombard and Italian Prune (fig. 11). Italian Prune, Agen, Sugar, and Imperial Epineuse constitute an important group of European plums with firm flesh and high sugar content suitable for use fresh or as dried prunes (fig. 12). Other varieties, such as Tragedy, Reine

Claude, Bradshaw, and Golden Drop, are used principally for canning and dessert plums.

The damsons (*Prunus insititia*) of the Old World are quite different from the domesticas. The trees are more upright, compact, and dwarfish, the leaves and flowers are smaller, and the fruits are small, round, and quite tart, so that they are especially suitable for preserves and jams. Varieties of this group are hardy, vigorous, and productive, and the trees make good stocks for other species, being adapted to a wide range of conditions and thriving even when they are neglected. The Shropshire (fig. 13) and French are important

Figure 13.—Shropshire, one of the most important varieties in the damson group of *Prunus insititia*. This small blue plum, like others belonging to this group, is used principally for preserves.

blue damsons in this country, while the yellow Mirabelles are popular in France. The group as a whole has certain valuable qualities that appear to have been overlooked in breeding investigations.

The Japanese plums (*Prunus salicina*) are relatively new to North America, but in the short time since their introduction they have been widely planted and now rank second to the domesticas in commercial production. The trees are more spreading in habit than the domesticas or damsons, and in leaf and fruit characters they are very different, resembling the native American plums. The fruits are very attractive and are characterized by a yellow ground color overlaid by various shades of red. In some varieties the flesh color is a striking red, whereas fruit of the domesticas and damsons is green or yellow. Some recent hybrids of the salicina group (fig. 14) show distinct superiority

Figure 14.—Plum hybrids. *A*, *Prunus salicina* hybrid, variety Apple. This red-fleshed variety illustrates the round shape of the varieties of this species. *B*, America, a hybrid between *P. munsoniana* and *P. salicina*. *C*, Hybrid resulting from a cross of the purple-leaved plum *P. cerasifera* var. *pissardii* with *P. salicina* variety Abundance.

in flavor and in commercial possibilities over the early importations. Varieties of this group appear to be widely adapted in this country except in the very coldest climates. While the quality is not equal to that of the best domesticas, the fresh fruit is delicious in its blend of flavors. The varieties cross readily with one another and with the native americanas. Among the first Japanese plums grown in this country, Kelsey, Burbank, Abundance, and Satsuma are typical. The trees are hardy and productive, and they tolerate a variety of soils as well as climatic conditions. They blossom early, and the flowers are sometimes killed by late spring frosts.

Among the plums native to North America are varieties that are different in fruit and tree characters from the plums of Europe and the Orient. Botanists have divided the native American plums into a number of species and subspecies. Many of them have numerous characteristics in common, so that they overlap somewhat in present horticultural groups and classifications. *Prunus americana* Marsh., the most important of the native species, has a wide range of adaptation in this country, extending from Maine to Florida, westward to Utah, and northwestward into Manitoba. The tree is small, not as vigorous as the European, and it has rough, shaggy, grayish bark. The fruit is red, reddish yellow, or reddish orange, of pleasant flavor and good quality, but it has a thick, tough skin, and the flesh clings to the pit. De Soto and Weaver are among the typical cultivated varieties of americanas.

Other American species of minor importance from a commercial standpoint but of interest to the fruit breeder are the native varieties of *Prunus hortulana* Bailey; the Chickasaw plum, *P. angustifolia* Marsh.; and the wild-goose plums, *P. munsoniana* Wight and Hedr., of the southeastern and south-central United States, of which Wild Goose and Robinson are important varieties (*3*, *32*).

Other species of plums growing in North America are the Canada plum, *Prunus nigra* Ait., which is adapted to the north-central United States and Canada; the small beach plum, *P. maritima* Marsh., which grows along the eastern seacoast; and the western or Pacific plum, *P. subcordata* Benth., which grows east of the Coast Range in southern Oregon and northern California.

Finally, mention should be made of the myrobalan plum (*Prunus cerasifera* Ehrh.), a native of Europe, and the Simon or apricot plum, *P. simonii* Carr., a native of China. The myrobalan plum has been used a great deal in this country as a rootstock. Varieties of *P. cerasifera* and *P. simonii* are noted for their ornamental foliage.

This great collection of varieties and species affords an excellent opportunity not only for studying genetic relationships but for the development of new varieties by breeding. The study of the inheritance of characters in plums has, however, not been very extensive. This may be due in part to the fact that many varieties of plums are self-unfruitful; that is, they do not set fruit with their own pollen. This presents a problem to the fruit grower as well as to the plum breeder. It is, of course, impossible to obtain an inbred progeny to study the inheritance of characters if the blossoms cannot be selfed. Fortunately for both the breeder and the fruit grower, fruits can be obtained by cross-pollination, and not all varieties are self-unfruitful.

Objectives in Plum Breeding

It is a well-recognized fact that plum culture in North America has gradually been declining during the last 20 years. The reason for this is the failure to keep pace with the demand for fruits of high quality. Varieties that were satisfactory 25 to 50 years ago in most cases do not appeal to persons who have a taste for fruits of high quality. However, many varieties are still prized in the home garden even though they are not profitable to the large producers.

An important objective of any plum-breeding program should be the production of varieties of higher quality adapted to the various fruit regions of the country. None of the domestica plums of high quality can be grown satisfactorily south of Virginia or in the vast regions of the southwestern and south-central United States. Native American species grow in this part of the country, but their adaptability must be combined with the higher quality of other varieties and species. Work has been started in this direction, but it has met with failure because domestica and americana varieties have different chromosome numbers, and so far crosses between them have not yielded viable seedlings.

Further study is also needed in the direction of artificially increasing desirable mutations in plums. In a few instances desirable bud sports have been discovered, and careful search should be made to locate others.

In addition to high quality, consideration must be given to vigor, hardiness, and productiveness. Much has been accomplished in developing and selecting winter-hardy varieties for the Great Plains region. Similar work is needed to develop varieties adapted to regions with hot, dry summers.

Genetic and cytological studies are of first importance in initiating a plum-breeding program. Among the self-compatible varieties there is a wealth of valuable material that can be used as foundation breeding stock. Even before methods are developed for increasing fruitfulness in crosses between species, there is opportunity for research on the material within many of the plum species growing in this country.

Breeding Methods

The methods of breeding that have been described for the peach apply equally well to the plum. The breeder is confronted with the same problem of protecting the emasculated flowers in order to lessen damage to the pistils. With varieties known to be completely self-incompatible, emasculation is of course unnecessary, and time can be saved by omitting this operation.

The problem of seed germination and the production of new seedlings likewise confronts the plum breeder. The seeds from many crosses prove nonviable, and methods need to be worked out whereby a greater percentage of seeds can be made to grow.

Work of Private Breeders

The first work on plum improvement in this country consisted of attempts to obtain better strains of the native American plums by domesticating seedlings and selecting those most promising for size,

flavor, and productiveness. The most extensive work in this direction seems to have been started by H. A. Terry, of Crescent, Iowa. From about 1860 until the time of his death in 1909 he had originated over 50 varieties from native species. While there is little information available as to the breeding methods or parents used, it is certain that he produced more new varieties than any private breeder since his time. Some of the more important varieties introduced by him are Gold, Hawkeye, Hammer, Downing, Crescent, and Terry.

Work on the breeding of plums was begun by C. G. Patten, a private breeder and a contemporary of Terry in the same State, at Charles City, Iowa, in 1867. He was impressed by the great number of native plums found growing in the wild, became interested in domesticating some of these, and selected the best for the prairie and upper Mississippi Valley regions. Hardiness or ability to withstand cold winters was a factor to be considered in the selection of varieties for that region. He worked with the American species. One of his best selections was tested by the Iowa Agricultural Experiment Station and was introduced as the Patten plum.

Beginning about 1870, J. W. Kerr, of Denton, Md., began the study and testing of a large number of varieties of plums. He likewise was interested in developing new varieties from native plums. Among the varieties introduced by him are Choptank, Sophie, and Maryland.

In California, Luther Burbank began his plum-breeding work about 1880, at Santa Rosa. He introduced and produced many desirable types. Among the important varieties he developed from seed imported from Japan are Burbank, Abundance, and Satsuma. He was particularly interested in the Japanese types and did much to popularize the varieties of this species in California, and to lay the foundations for their later testing and use as important commercial varieties in that State. He likewise made a number of crosses between *Prunus salicina* and other species, producing Climax, Bartlett, and Wickson from *P. salicina* × *simonii*, and America (fig. 14) and Golden from *P. munsoniana* × *salicina*. Other varieties introduced that have been grown commercially in California are Giant, Splendor, Standard, Santa Rosa, Formosa, and Gaviota.

Hedrick and associates (*19, p. 170–171*) make the following comment on Burbank's work:

One cannot briefly catalog the new forms of plants that have gone forth from his private place in California; they must number well into the hundreds; his biographer, in 1905, said that Mr. Burbank has worked with over two thousand five hundred distinct species (Harwood, W. S., New Creations in Plant Life I. 1905). Among these have been practically all of the species of plums now under cultivation, from which have been obtained, according to Mr. Burbank, hundreds of thousands of plum-seedlings of which the breeder has selected a score or more of very distinct sorts, all interesting and a few of them very valuable. The many other fruits, flowers and forage plants which Mr. Burbank has sent out, each involving the handling of countless seedlings, cannot be mentioned here. Nor can his methods and results be discussed, except to say that in them he is a unique figure in plant-breeding and that they have been such that he has exercised a powerful influence toward the improvement of plants. The practical results of Mr. Burbank's work have been as great or greater than those secured by any other person in plant-breeding, yet they have been magnified out of all bounds in the popular press and his work has been caricatured by calling the man a wizard and ascribing to him occult knowledge. Of the plants introduced by Mr. Burbank

the proportion of really valuable commercial ones seems now to be small, but what he has done cannot be measured by money values; he has awakened universal interest in plant-breeding; has demonstrated that things unheard of before his time can be done with plants; and, all in all, his contributions in new forms of plants to horticulture and agriculture, in their intrinsic and educational value, make him the master worker of the times in improving plants.[6]

Millard W. Sharp, of Vacaville, Calif., in more recent years has produced and introduced several plum varieties. The method he used was to top-work many varieties into a single tree, allow free crossing, plant the seed, and make intensive selection of the resulting seedlings. Of the varieties he introduced, Sharky and Becky Smith have attained commercial importance.

Plum-breeding work has also been undertaken by Albert F. Etter and August Etter at Ettersburg, Calif. In recent years they have used as parents for hybrids Wild Goose, Marianna, Golden Drop, Agen (French prune), Japanese varieties, and Sierra, a peculiar domestica type that grows wild in Trinity County, Calif.; two wild native plums from Mongolia, and the native plums of Kansas. In all, this includes about a dozen species. The outstanding ability to produce new forms shown by the Sierra, the Kansas, and the Trinity plums is of particular interest. The Sierra hybrids exhibit wide variations in tree and fruit characters. These are under test at the present time, but no varieties have been introduced.

Harlan Rockhill, of Conrad, Iowa, has been engaged in fruit breeding since 1895. Among his recent selections are some promising plum hybrids from crosses of Waneta × Apex, Waneta × Moorpark, No. 10 × P. I. 78519, Waneta dwarf seedling × Apex × P. I. 78519. The last-mentioned cross is reported to be particularly hardy in wood and bud, having withstood temperatures of −26° to −36° F. during the winter of 1935–36. This variety and others are being tested further.

Plum Breeding at State and Federal Stations

South Dakota

Work was undertaken at the South Dakota Agricultural Experiment Station in 1895 by Hansen (*15*) in an attempt to select American varieties of plum that would be satisfactory for the Great Plains region. Up to 1937 fully 10,000 native plum seedlings of *Prunus americana* had been grown in an endeavor to find native seedlings better in size and quality than those already grown. Wastesa, Yuteca, Zekanta, Huya, and Topa were selected and named. Yuteca is large; Wastesa is outstanding for size and quality. Hansen attempted to introduce quality into the native plums by crossing these into a number of other species such as peach, cherry, and apricot, as well as with other varieties of plum. The following is a list of crosses made, together with notes on the progeny:

Prunus besseyi Bailey (Bessey cherry or western sand cherry) × apricot plum *P. simonii* Carr. Not hardy, fruits sparingly. One variety only named but the trees have since been discarded.

P. besseyi × Japanese plum (*P. salicina* Lindl.). Progeny highly fertile, hardy. widely cultivated. Among varieties named are Opata, Sapa, and Oka.

P. besseyi × native plum (*P. americana* Marsh.). Two varieties named, Sansoto and Cheresoto, which are highly fertile.

[6] Burbank's achievements and limitations have also been summed up critically by Jones (*22*).

P. besseyi × Apricot (*P. armeniaca* L.). Progeny very shy bearers.

P. besseyi × peach (*P. persica*). Flowers of hybrid (Kamdesa) were sterile.

P. americana × *simonii*. Three varieties named, Toka, Hanska, and Kaga, which are strong pollinators for other varieties. The fruit is fragrant, flesh firm, and of excellent quality.

P. simonii × *americana*. This cross produced Tokata: the fruit is large and of excellent flavor. The seedlings of this cross require cross-pollination.

P. salicina × *americana*. The progeny of this cross is highly fertile. Five varieties have been introduced and widely cultivated—Waneta, Kahinta, Tawena, Oziya, Tecumseh.

P. americana × *salicina*, the reciprocal of the former species cross, has yielded many choice hybrids which are self-fertile and interfertile.

Canada plum (*P. nigra* Ait.) × *P. salicina*. This combination has yielded the varieties Cree and Pembina.

P. salicina × *nigra* has given the variety Ojibwa.

From Canada plum, *Prunus nigra*, pure selections have been made and introduced as Assiniboin and Winnipeg.

Since 1895 selections have been made from over a million seedlings of *Prunus besseyi*. The thirteenth generation has now fruited.

New York

At the New York (State) Agricultural Experiment Station, Geneva, plum breeding was started as early as 1893, when a few open-pollinated seedlings were grown. Under test the seedlings proved to be of no commercial value. From 1908, when the first crosses were made at the New York station, up to the present time, 78 varieties, 6 seedlings, and 7 United States Department of Agriculture introductions have been used in breeding work, and 546 crosses, 16 selfs, and 26 open pollinations have been made. Only 519 seedlings have been planted in the orchard. The set of seed has not been high, and there were serious losses between the time of harvesting the seed and planting. Considerable difficulty has sometimes been experienced in getting the seeds to grow. A few Japanese plums (*Prunus salicina*) have given seedlings, but no seedlings have been obtained from the early-maturing European or domestica group.

It has been the experience in the plum-breeding work at Geneva that it is difficult to obtain large quantities of seed from hand-pollinated trees. The flowering season is usually brief and there is often a high mortality of blossoms. It has been suggested that the use of tents and bees for pollination would be the economical method for securing large numbers. The comparatively few seedlings that have fruited indicate that it is not difficult to make rapid progress in plum improvement. The large-fruited, attractive, poor-quality Grand Duke has given promising new varieties when crossed with high-quality Golden Drop and Agen. Imperial Epineuse and Pearl have also imparted good quality to a high degree in crosses. The varieties that have been used most extensively and the number of times they have been used are: Abundance 23, Agen 23, Albion 8, Archduke 8, Beauty 17, Burbank 57, Clyman 11, Formosa 13, Golden Drop 8, Grand Duke 23, Hall 12, Imperial Epineuse 30, Jefferson 8, Miller Superb 10, Oullins 22, Reine Claude 19, Rivers Early 12, Santa Rosa 16, Shiro 10, Stanley 16, Tragedy 8, and Yellow Egg 28. A list of plum varieties introduced by the New York station is given in table 4.

TABLE 4.—*Plum varieties introduced by the New York (State) Agricultural Experiment Station*

Variety introduced	Parentage	When crossed	Year introduced	Purpose
Albion	Golden Drop × Grand Duke	1908	1929	Very late season.
American Mirabelle	Imperial Epineuse × Mirabelle.	1911	1925	Home and roadside market.
Hall	Golden Drop× Grand Duke	1908	1925	Do.
Stanley	Agen × Grand Duke	1913	1926	Commercial market.

The opinion is expressed by Richard Wellington that by intercrossing hybrids such as Hall, Albion, and Stanley, and by crossing them on high-quality plums such as Imperial Epineuse, varieties of better quality should be obtained. A large number of varieties and species of plums are grown on the grounds of the New York station as basic material for the production of better varieties.

California

The California Agricultural Experiment Station at Davis has grown a large number of varieties of plums on the station grounds. These have been used in studies on pollination and variety behavior under California conditions. Because of the demand for improved varieties of plums, breeding work was started in 1934. Poor germination of plum seeds has been an important factor in slowing down the production of seedlings. All the species of plums grown in North America, together with some miscellaneous species, are being utilized. A complete list is given in the appendix. Genetic and cytological work on interspecific crosses is under way.

Iowa

At the Iowa Agricultural Experiment Station a large number of plum crosses have been made, using *Prunus americana*, *P. salicina*, *P. domestica*, and *P. maritima;* also *P. armeniaca*. Interspecific hybrids between *P. americana* and *P. salicina* are grown, and 180 trees resulting from crosses between species and varieties are now being grown in the nursery at Ames. These crosses were made during the period 1931–33. Varieties used as pollen parents and the number of times they were used are: Elliot 5, Hennepin 4, Japex 2, Monitor 2, Sapa 5, Waneta 6, and Anthony, Zumbra, Red Wing, and Burbank each 1. Crosses between the plum and the Russian and Moorpark apricots have been made. Greenhouse trees are being utilized in the breeding work with *Prunus*, and many hundreds of nonfruiting crosses not listed above have been made on them. The interspecific hybrids that prove to be fertile will be preserved for future crossing. The trees are brought into the greenhouse about January 10 and are ready for crossing about 3 or 4 weeks later.

Minnesota

Plum-breeding work at the Minnesota Agricultural Experiment Station was begun in 1889 at University Farm by S. B. Green, horticulturist. In the same year breeding work was also started by E. H. S.

Dartt at Owatonna Tree Station, a branch station of the University. This work consisted of selection of open-pollinated seed from superior native varieties. More extensive and systematic work began in 1907 with the establishment of the present University of Minnesota Fruit Breeding Farm. Up to the present 20 varieties have been introduced—Anoka, Elliot, Ember, Golden Rod, Hennepin, La Crescent, Mendota, Monitor, Mound, Newport, Nicollet, Radisson, Red Wing, St. Anthony, Superior, Tonka, Underwood, Waconia, Winona, and Zumbra. They are of special interest for the upper Mississippi River Valley area because of their winter hardiness, but are worthy of testing in other sections also, and they should provide material for additional studies. Detailed descriptions of these varieties, their parentage, and the dates of introduction are given in the appendix, which also includes a list of the varieties now being used in further breeding studies.

A considerable amount of breeding material is available involving various species of native and foreign plums and other closely related species of stone fruits. Since winter hardiness is a primary requisite, all breeding material is subjected to severe field tests to determine its resistance to cold.

Federal Field Stations

A number of varieties and specific crosses of plum have been made in cooperative investigations by the Bureau of Plant Industry, United States Department of Agriculture, and Leland Stanford Junior University at Palo Alto, Calif. The following varieties and species have been used as seed parents: Agen, Anita × Sugar, Becky Smith, Burbank, Clyman, Duarte, Fremonti, Giant, Golden Drop, Imperial Epineuse, Improved French, Methley, Pond, Sergeant, Tragedy, Wickson, and *Prunus bokhariensis* Royle. In addition the following varieties have been used as pollen parents: Sugar, Gaviota, Formosa, Santa Rosa, Beauty, Satsuma, Standard, and Tunis. Two promising hybrids, Methley × Wickson and Wickson × Santa Rosa, have been selected. The latter variety is a delicious plum, representing a particularly fine blend of flavors and ripening just after Santa Rosa. The tree is productive and in preliminary tests seems to be well adapted to California conditions. A complete list of plum hybrids produced is given in the appendix to this section.

At the Northern Great Plains Field Station, Mandan, N. Dak., more breeding work has been done with plums than with any other fruit except apples. Thousands of seedlings have been grown from the native wild plum and cultivated varieties. A great deal of variation is to be found within the *Prunus americana* species, and over 50 selections were made, some of which were propagated for a more thorough test. A few of these are ready for more extensive testing in the northern Great Plains area. Of late years a large number of Japanese hybrid seedlings have been grown. Hybridizing work has been in progress, using hardy *P. americana* and *P. nigra* varieties, these being crossed with Japanese varieties, domestica varieties, *P. simonii*, *P. tomentosa* Thunb., apricots, and cherries, and with such hybrid plum varieties as Waneta, Underwood, and Sapa. Some of the progenies are now bearing fruit, and a few selections have been made.

Plum Breeding in Canada

Plum breeding at the Horticultural Experiment Station, Vineland, Canada, was started in 1913. From 1913 to 1935, 4,240 seedlings were grown. Seeds were planted from 57 open pollinations and 35 crosses. Out of this number 16 had horticultural value. During the period 1931 to 1933, 860 seedlings were grown from crosses in which Imperial Epineuse was used as the female parent, and Grand Duke, Coe Fellenberg, and President have been used as pollen parents. The object of the cross was to produce a high-quality blue plum for the export trade.

Genetic and Cytological Studies of the Plum [7]

Experiments with plums were begun at the John Innes Horticultural Institution in England by W. J. Backhouse and Crane (*8*) in 1911, to investigate the genetic composition of plum trees by raising selfed offspring. The characters studied were (1) hairiness of shoots, leaf petioles, and fruits; (2) smoothness of bark and size and shape of leaves; (3) habit of growth of tree; and (4) bark and fruit color.

All the varieties of plums studied with hairy wood surface proved to be heterozygous for that character. Serrate leaf character proved to be homozygous in the Pershore variety, and crenate leaf margin homozygous in the Czar family. The irregular margin appeared to be heterozygous in varieties possessing this character.

Flesh color varied. Varieties in which yellow was the predominating flesh color have, when selfed, given seedlings with a green, and a wholly yellow flesh.

As to fruit size and shape, many of the differences were recognized as doubtless quantitative. The oblate fruit of Early Transparent, for example, and the pyriform fruit of the Pershore variety proved to be homozygous for these forms. With some selfed families, length and shape varied in the progeny.

Wellington (*32*) has carried on extensive investigations at the New York (State) Agricultural Experiment Station in breeding and genetic studies with a number of plum varieties and species. He found the oval fruit shape of *Prunus domestica* dominant to oblate. Thick bloom on the surface of the fruit is dominant to thin bloom. Yellow color is recessive to red, purple, and black. The freestone character is recessive to clingstone. Many varieties are heterozygous for the freestone character, freestones being obtained from the cling and semicling parents.

Some varieties of our domestica plums set fruit with their own pollen; others are partially self-incompatible, while a third group fail entirely with their own pollen. Insititia varieties grown in this country are self-fruitful. Nearly all of the varieties of the Japanese group are self-sterile.

Tufts has found the following important varieties of domestica plums to be self-unfruitful in California: Clyman, Tragedy, Imperial Epineuse, President, Standard, Sergeant, Washington, Jefferson, Quackenboss, Diamond, and Silver. Self-fruitful varieties were

Agen, Giant, Pond (partially), Grand Duke (partially), California Blue, Yellow Egg, and Sugar.

The following Japanese and hybrid plums were self-unfruitful in California: Abundance, Burbank, Duarte, El Dorado, Formosa, Gaviota, Kelsey, Prize, Satsuma, Sultan, Upright, and Wickson. Methley, Climax, Beauty, and Santa Rosa are partially self-fertile. Formosa and Gaviota were also found to be interunfruitful. The Tragedy plum will fertilize several Japanese varieties but is not fertilized by them.

Crane and Lawrence (*10*) observed that certain of the domestica plums were completely self-and cross-incompatible, while others, such as President and Late Orange, were reciprocally incompatible but set fruit when pollinated with Green Gage (probably Reine Claude). Early Rivers, when pollinated by Blue Rock, set a full crop, while in the reciprocal cross only a few fruits set. Varieties such as Golden Drop, Coe Violet, and Jefferson, were found to be completely self- and cross-incompatible (*9*).

Incompatibility Due to Genetic Make-up

Experiments by a number of investigators, East (*13*), Lehmann (*24*), and others, have shown that sterility is determined by genes just as are morphological characters. East designated these genes S, and they form a multiple allelomorphic series, S_1, S_2, S_3, etc. As in the case of other allelomorphs, any two may be carried by a given plant. While this concept is based on the results of studies with *Nicotiana*, it fits into the observations made on stone fruits and explains incompatibility in plums and cherries. The essential features of the genetic behavior of incompatibility is that pollen cannot function in the style of a plant carrying the same incompatibility factors as the pollen. Self-pollinations or cross-pollinations among individuals carrying the same sterility genes fail because either the pollen tubes grow so slowly that in normal cases they are unable to reach the ovules in time to effect fertilization, or the growth of the pollen tube is inhibited in the stylar tissue. Consequently, groups of individuals occur within which all cross- and self-pollination fails to effect fertilization. Thus, individuals of the constitution S_1, S_2, cannot be fertilized by S_1 or S_2 pollen. If, however, such individuals are crossed by S_3 S_4, both the S_3 and S_4 pollen can penetrate the style of the mother and effect fertilization. It will be seen that the offspring from such a cross, allowing all combinations possible, will constitute four intrasterile, interfertile groups of the composition S_1 S_3, S_1 S_4, S_2 S_3, S_2 S_4.

With certain of our plum varieties, of either the Japanese or the domestica species, self-unfruitfulness occurs when those varieties carry a gene for incompatibility. Likewise, varieties would be cross-unfruitful if both parents carried the same genes for incompatibility.

Chromosome Numbers in the Plums

In the genus *Prunus* the basic chromosome number is 8. All the varieties examined among the myrobalan plums (*P. cerasifera*), American plums (*P. americana*), and Japanese plums (*P. salicina*)

show the diploid number ($2n$) to be 16. Other species, notably the sloe (*P. spinosa* L.), have the tetraploid number or 32 chromosomes, and a still greater number (48) is found in the important groups of European plums (*P. domestica*) and the damsons (*P. insititia*).

Hybrids of *Prunus domestica* (48) × *P. cerasifera* (16), and *P. insititia* (48) × *P. spinosa* (32) have the intermediate chromosome numbers, 32 and 40, respectively.

According to Crane and Lawrence (*10*), the hybrids that they have obtained between *Prunus domestica* and *P. insititia*, both hexaploid, have always been completely interfertile; but from crosses between diploid and polyploid, and different polyploid forms, such as *P. domestica* × *P. cerasifera* and *P. insititia* × *P. spinosa*, fruits with viable seeds are rarely produced. Crosses between damsons and other varieties of *P. insititia* and *P. domestica* when attempted have always set fruit and developed good seeds freely. Wellington has also made many interspecific crosses. Crosses have been made successfully between *P. domestica* and *P. insititia*. With a large number of other interspecific crosses, however, involving *P. domestica* × *P. armeniaca* and its reciprocal; *P. domestica* × *P. tomentosa*, and *P. domestica* × *P. americana*, few fruits were obtained or the seeds failed to grow. Insofar as is known, triploid varieties of *Prunus* are found only as ornamentals, their degree of sterility being too high to enable them to be grown for their fruits.

Appendix (Plum)

Table 5.—*Locations of plum-breeding work and names of workers in United States and other countries*

State or country, institution, and location	Early workers	Workers actively engaged at present
California:		
Agricultural Experiment Station, Davis.	E. J. Wickson, W. L. Howard, A. H. Hendrickson.	W. P. Tufts, E. C. Hughes.
U. S. Department of Agriculture, Davis.	----------	J. R. King.
U. S. Department of Agriculture, Palo Alto.	----------	W. F. Wight.
Iowa:		
Agricultural Experiment Station, Ames.	S. A. Beach	T. J. Maney.
Minnesota:		
Agricultural Experiment Station, University Farm, St. Paul.	Charles Haralson, M. J. Dorsey, W. S. Valleau, J. H. Beaumont.	W. H. Alderman, A. N. Wilcox.
New York:		
Agricultural Experiment Station, Geneva.	U. P. Hedrick, W. H. Alderman, M. J. Dorsey.	R. Wellington, Olaf Einset.
North Dakota:		
U. S. Department of Agriculture, Northern Great Plains Field Station, Mandan.	Max Pfaender	William P. Baird.
South Dakota:		
Agricultural Experiment Station, Brookings.	N. E. Hansen	N. E. Hansen.
Canada:		
Horticultural Experiment Station, Vineland, Ontario.	----------	F. E. Palmer, G. H. Dickson.
England:		
John Innes Horticultural Institution, Merton.	----------	W. J. C. Lawrence.
Australia:		
Department of Agriculture, Sydney, New South Wales.	----------	H. Wenholz.

Table 6.—*Varieties used in plum breeding at the University of Minnesota*

Parentage	Period during which crosses were made	Total seedlings grown	Seedlings of horticultural value	Apparent value of parents used
		Number	*Number*	
Assiniboin Open	1915	208	16	Fair
Assiniboin × Surprise	1925–27	229		
Reciprocal cross	1926	181		Poor
Burbank × Assiniboin	1920–26	26		
Reciprocal cross	1925–26	6		
Burbank × De Soto	1913	43	3	
Reciprocal cross	1912	27	1	Fair
Burbank × Kaga	1920–25	233	33	Good
Reciprocal cross	1920–26	15		
Burbank × Older	1927	10		
Reciprocal cross	1923 27	14		
Burbank Open	1923 26	39	3	Fair
Burbank × *Prunus americana*	1913 26	279	28	Good
Reciprocal cross	1922–27	70	1	
Burbank × Red Wing	1920	19	1	Fair
Reciprocal cross	1920	2	1	
Burbank × sand cherry	1920	72	2	Fair
Reciprocal cross	1921	10		
Burbank (sand cherry × Climax)	1920	30		
Reciprocal cross	1921	48	2	Fair
Burbank × S Dak No 27	1921 26	9		
Reciprocal cross	1924 26	89	1	
Burbank × Surprise	1924–26	13		
Reciprocal cross	1921 26	10		
Burbank × Wakapa	1921	1		
Reciprocal cross	1912 21	20	2	
Burbank × Wolf	1912–26	77	6	Good
Reciprocal cross	1923–27	28		
(Burbank × Wolf) open	1912	31		
Compass × Burbank	1912	60	2	Fair
Compass × Climax	1912	107	5	Do
Compass × Formosa	1912	37	1	Do
Early Red × *P americana*	1912	21		
Elliot × Mendota	1922 27	25		
Emerald × Assiniboin	1920	179		Poor
Emerald × Tonka	1920–21	30		
Emerald × (Wyant × Gold)	1924	5		
Reciprocal cross	1924	15		
Omaha × Burbank	1912	39	4	Good
Omaha × Santa Rosa	1912	23	2	
Omaha × Winnipeg	1912	20		
(Pin cherry × sweet cherry) × sand cherry or sand cherry hybrid	1912	81	11	Good
Red Wing × Assiniboin	1920–21	156		
Red Wing × Kaga	1920–23	54	2	Fair
Reciprocal cross	1920	3		
Sand cherry × Climax	1912	60	5	Good
(Sand cherry × Climax) × Sapa	1920	21	1	
(Sand cherry × Climax) × Tonka	1920–21	25		
Reciprocal cross	1920		3	
Sand cherry × Formosa	1912	27	4	Good
Sapa × Surprise	1924	24		
Satsuma × Compass	1912	26		
Reciprocal cross	1912	29	1	
Shiro × *P americana*	1912	21	4	Good
Shiro × S Dak No 33	1913	31	7	Do
Reciprocal cross	1912	1		
Shiro × Winnipeg	1912	38	7	Do
Reciprocal cross	1912	1	1	
S Dak No 27 × Monarch	1924 26	50		
S Dak No 27 × October Purple	1924	23		
Reciprocal cross	1924	1		
S Dak No 27 × Santa Rosa	1925–26	91	7	Good
Stella, open	1912–15	72	1	
Tonka × Assiniboin	1920–25	209		Poor
Tonka × Red Wing	1920	33		
Reciprocal cross	1920	3		
Wakapa × First	1912	45		
Wakapa × *P cerasifera pissardii*	1912	28		
Wakapa × Wickson	1921	26		
Reciprocal cross	1921	3		
Wakapa × Wyant	1912	22		
Winnipeg, open	1915	93	4	Fair

TABLE 6.—*Varieties used in plum breeding at the University of Minnesota*—Continued

Parentage	Period during which crosses were made	Total seedlings grown	Seedlings of horticultural value	Apparent value of parents used
		Number	*Number*	
Zekanta × *P americana*	1912	20	2	
Minn No 2 (Burbank × Wolf) × Burbank	1924	18		
Reciprocal cross	1924	18		
Minn No 6 (Burbank × Wolf) × Terry	1923	21		
Minn No 16 (Abundance × Wolf), open	1912	30		
Minn No 35 (Abundance × Wolf) × Burbank	1920	10		
Reciprocal cross	1920	97	5	Fair
Minn No 55 (Abundance × Wolf) × No 57 (Shiro × Winnipeg)	1924 26	64		Poor
Reciprocal cross	1924 26	65		Do
Minn No 55 (Abundance × Wolf) × No 63 (Shiro × Winnipeg)	1924 26	46		
Minn No 55 (Abundance × Wolf) × No 90 (Burbank × Wolf) 21	1924	87	2	
Minn No 55 (Abundance × Wolf) × No 104 (Burbank × ?)	1924	25		
Minn No 59 (Shiro × Winnipeg) × No 57 (Shiro × Winnipeg)	1924 27	64		
Reciprocal cross	1925 26	4		
Minn No 62 (Shiro × Burbank) × No 57 (Shiro × Winnipeg)	1924 25	63		
Minn No 66 (Shiro × Wolf) × No 65 (Shiro × Wolf)	1924–25	25		
Reciprocal cross	1925	1		
Minn No 76 (Burbank × *P americana*) × No 62 (Shiro × Burbank)	1925–26	23		
Minn No 84 (S Dak No 33 × Shiro) × No 77 (Shiro × native)	1924–26	43		
Minn No 90 (Tonka open) × No 55 (Abundance × Wolf)	1924	111		Poor
Minn No 92 (Omaha × Wyant) × No 74 (Santa Rosa × Bursota × Winnipeg)	1924	95		Do
Reciprocal cross		2		
Minn No 92 (Omaha × Wyant) × No 106 (Omaha × Santa Rosa)	1924–25	64		
Reciprocal cross	1925	6		
Minn No 98 (?) × Winona, reciprocal cross	1923	24	2	
Minn No 98 (?) × No 96 (Zekanta × apricot)	1925	20		
Minn No 106 (Omaha × Wyant) × No 55 (Abundance × Wolf)	1926	36		

TABLE 7.—*Plum introductions of the Minnesota Agricultural Experiment Station*

Variety	Parentage	When crossed or seed collected	When introduced	Descriptive notes (special value and superior characters)	Estimated acreage now planted
Anoka (Minn No 118)	Burbank × De Soto	1913	1922	Hardy, productive	Small
Elliot (Minn No 8)	Probably apple plum × *Prunus americana*	1907	1920	Very hardy, productive good quality, late season	175 acres
Ember (Minn No 83)	Shiro × S Dak No 33	1913	1936	High quality late season long-keeping quality, exceptional adherence to tree	Small
Golden Rod (Minn No 120)	Shiro × Howard Yellow	1913	1923	Vigorous tree, larger firm yellow fruit (Variety a shy bearer)	50 acres
Hennepin (Minn No 132)	Satsuma × *P americana*	1911	1923	Hardy, productive red flesh	Small
La Crescent (Minn No 109)	Shiro × Howard Yellow	1913	1923	Very high quality large, vigorous tree	100 acres
Mendota (Minn No 5)	Burbank × Wolf	1908	1924	Very large fruit, good quality	Small
Monitor (Minn No 70)	Probably Burbank × *P americana*	1912	1920	Large, high-quality fruit, hardy, regularly productive	300 acres
Mound (Minn No 50)	Burbank × Wolf	1908	1922	Large size of fruit productive	[1].
Newport (Minn No 116)	Omaha × Pissardii	1913	1923	An ornamental with purple foliage	25 acres
Nicollet	(*P avium* × *pensylvanica*) [2]	1912	1925	Dwarf, bushlike, fruit similar	50 acres

[1] All in scattered landscape plantings
[2] Open pollen parent is *Prunus besseyi* or a hybrid of this species

TABLE 7.—*Plum introductions of the Minnesota Agricultural Experiment Station*—Con.

Variety	Parentage	When crossed or seed collected	When introduced	Descriptive notes (special value and superior characters)	Estimated acreage now planted
Radisson (Minn. No. 157).	*P. salicina* × *americana*.	1908	1925	Early-maturing high-quality fruit; adapted to northern locations.	Small.
Red Wing (Minn. No. 12).	Burbank × Wolf..	1908	1920	Large high-quality fruit; exceptional freestone.	250 acres.
St. Anthony (Minn. No. 145).	*P. besseyi* (or hybrid) × Satsuma.	1912	1923	Very hardy and productive; red flesh.	50 acres.
Superior (Minn. No. 194).	Burbank × Kaga..	1920	1932	Very productive and early bearing; fruit very large, firm, excellent quality.	100 acres.
Tonka (Minn. No. 21)	Burbank × Wolf...	1908	1920	Very productive; firm flesh; high quality.	300 acres.
Underwood (Minn No. 91).	Shiro × Wyant.	1911	1920	Very vigorous; hardy; productive; early ripening; excellent quality.	500 acres.
Waconia (Minn. No. 10).	Burbank × Wolf..	1908	1923	Hardy; productive; quality only fair.	Small.
Winona (Minn. No. 80).	*P. salicina* × *americana*.	1909	1922	Hardy; productive; high quality; late season.	Do.
Zumbra..............	(*P. avium* × *pensylvanica*).[2]	1912	1920	Dwarf, bushlike; very productive; excellent culinary quality.	100 acres.

[2] Open pollen parent is *Prunus besseyi* or a hybrid of this species.

Plum Hybrids Produced and Under Test in Breeding Investigations of United States Department of Agriculture and Leland Stanford Junior University at Palo Alto, Calif.

Year	Parents
1921	Agen × Anita.
1931	(Agen × Anita 18–31) × Imperial Epineuse.
1929	Agen × (Coe × Sugar).
1922	Agen × Standard.
1920	Agen × Sugar.
1931	(Agen × Sugar 18–12) × Imperial Epineuse.
1920	Anita × Sugar.
1931–32	(Anita × Sugar) × Agen.
1934	Becky Smith × Tunis.
1920	*Prunus bokhariensis* × Methley.
1921	*P. bokhariensis* × Sugar.
1920	*P. bokhariensis* × Wickson.
1934	Burbank × Formosa.
1932	Burbank × (*P. fremonti* × *cerasifera pissardii* 11–3 [3]).
1933	Burbank 2010 × Gaviota.
1932	Burbank × Satsuma.
1932	Clyman 12010 × (Anita × Sugar 18–45).
1934	Duarte × Santa Roas.
1933	(*P. fremonti* × *cerasifera pissardii* 11–31) × *P. bokhariensis* × Methley 6–6).
1924–26	Giant × Imperial Epineuse.
1919	Golden Drop (Coe) × Sugar.
1931	(Golden Drop (Coe) × Sugar) × Imperial Epineuse.
1926	Imperial Epineuse × Improved French.
1924–26	Imperial Epineuse × Tragedy or Agen.
1926	Improved French × Tragedy.
1920	Methley × Wickson.
1935	(Methley × Wickson 11–56) × Beauty.
1932–33	(Methley × Wickson 11–54) × Satsuma.

[3] The hyphenated numbers following certain varietal names refer to row and tree locations.

1933	(Methley × Wickson 11–57) × (Wickson × Santa Rosa 15–23).
1921	Pond × Agen.
1926	Sergeant × Improved French.
1926	Tragedy × Clyman.
1921	Wickson × *P. bokhariensis*.
1933	Wickson 7–24 × (*P. bokhariensis* × Methley 6–6).
1921	Wickson × Santa Rosa.
1935	Wickson × (Wickson × *P. bokhariensis* 15–21).

Plum Material at the California Agricultural Experiment Station, Davis, Calif.[9]

Prunus domestica:
- Admiral
- Agen (French)
- Altharm
- Anita
- Archduke
- Arctic
- Austrian Prune
- Autumn Compote
- Bavay
- Bird Prune
- Bittern
- Black French
- Black Prince
- Blue Rock
- Boddaert
- Bradshaw
- Bridge
- Bulgarian
- Burton Prune
- California Blue
- California Red
- Callas
- Champion (Burton)
- Champion (Villa)
- Clairac Mammoth
- Clyman
- Coates 1401
- Coates 1403
- Coates 1414
- Coates 1418
- Columbia
- Communis
- Crimson Drop
- Curlew
- Czar
- De Caisne
- De Montfort
- Denbigh
- Diamond
- Diana
- Dosch
- Double × French
- Duane
- Duchess
- Dulce
- Dunlap

Prunus domestica—Con.
- Earliana
- Early Favorite
- Early Golden Drop
- Early Royal
- Early Tragedy
- Emilie
- Empire
- Femonzi
- Field
- Florence
- Fraulein
- German Prune
- Giant
- Gill
- Golden Drop
- Golden Prune
- Golden Transparent
- Goliath
- Grand Duke
- Green Gage
- Gueii
- Hall
- Hand
- Hector
- Heron
- Honori
- Hulings
- Hungarian
- Ickworth
- Imperial
- Imperial Gage
- Italian Prune
- Jefferson
- Junction City Prune
- June Fourth
- Kaiser
- Kimball
- Kirke
- Large English
- Late Orange
- Late Orleans
- Late Tragedy
- Leighton Italian
- Liberty Prune
- Lincoln

Prunus domestica—Con.
- Lombard
- Long Green
- Long Stem
- Los Angeles
- Lucombe
- Mallard
- Margaret
- McLaughlin
- Middleburg
- Miller Superb
- Missouri Green Gage
- Monarch
- Monk
- Mount Royal
- Moyer
- Napa
- Newark
- New Oregon Prune
- Oullins
- Pacific
- Palatine
- Papagone Prune (P. I. 40498)
- Peach
- Pearl
- Peters
- Pond
- President
- Primate
- Prinlow
- Purple Gage
- Quackenboss
- Rayburn
- Reuter Early Italian
- St. George
- St. Jean
- St. Martin
- Sannois
- Sergeant
- Sharpe Imperial
- Shipper
- Silver Prune
- Smith Orleans
- Smith Late
- Splendor

[9] This list of variety names is approximately as submitted by the California station. The names are those under which the material is recorded, and not all of them are necessarily intended as authentic variety names. The list apparently contains a considerable number of names representing local strains and other names that do not conform to the generally accepted code of nomenclature. It is impracticable to attempt to bring the nomenclature in all cases into harmony with the code, therefore only a few changes representing obvious differences have been made

Prunus domestica—Con.
- Standard
- Stanley
- Stark Green Gage
- Steward Prune
- Stint
- Stuart
- Sugar
- Super Prune
- Swan
- Sweetest
- Tardeva de Moleta
- Tatge
- Tennant
- Tragedy
- True Blue
- Tulare
- Turkish Prune (synonym of Italian Prune)
- $2000 Prune
- Uncle Ben
- Ungarish
- Victoria
- Voronesh
- Wales
- Washington
- Wilhelmina
- Williamson Tragedy
- Yakima
- Yellow Egg
- Yellow Gage
- Yellow Imperial
- York State Prune
- Zucheriva del Vesuvia

Prunus salicina:
- Abundance
- Alpha
- Amador
- Apex
- Beauty
- Becky Smith
- Best's Hybrid
- Blood Plum
- Blue Gown
- Botan
- Burbank
- Burton
- Chabot
- Clarice
- Collie
- Del Norte
- Earliest of All
- Engre
- Extra Early Satsuma
- Florida
- Georgeson
- Hale
- IXL
- Kelsey
- McRea
- Miss Edith

Prunus salicina—Con.
- Occident
- October
- Ogon
- Pasha
- Purple Flesh
- Raisin
- Red June
- Sachem
- Santa Rosa
- San Francisco
- Satsuma
- Schattenburg
- Sherkey
- Strang
- Tribble Early Beauty
- Ulatis
- Valleda
- Willard
- Wilson
- Wright Early (P. I. 43180)
- Wright Purple (P I. 43181)

Prunus americana:
- Admiral Schley
- Advance
- Desoto
- Golden Queen
- Hawkeye
- Klondike
- Muncy
- New Ulm
- Quaker
- Skuyu
- Stoddard
- Weaver
- Wolf
- Wood
- Wyant

Prunus americana var. *mollis* Torr. and Gray:
- Gloria
- Terry

Prunus nigra:
- Aitken
- Cheney
- Eureka

Plumcots (so-called):
- Francis I
- Poe Royal Cot Plum
- Rutland
- Sharpe
- Smith
- Sparks
- Stanford
- Triumph
- Velvet

Prunus insititia:
- Big Mackey
- California Wild

Prunus insititia—Con.
- Crittenden
- Damson Free
- Damson Majestic
- French damson
- Frogmore
- King damson
- Merryweathers
- St. Julien
- Shropshire
- White damson

Prunus munsoniana:
- Clifford
- Downing
- Early June
- Freestone Goose
- Jewell
- Late Goose
- Monthalia
- Newman
- Oxheart
- Poole Pride
- Pottawattomie
- Wildgoose Improved
- Wooten

Native plum:
- Zekanta

Prunus hortulana:
- Forest Garden
- Golden Beauty
- Minco
- Robinson
- Surprise
- Wayland

Prunus hortulana var. *mineri* Bailey:
- Miner

Prunus bokhariensis:
- P. I. 40224

Species unknown:
- May Queen
- Progressive
- Superior

Prunus cerasifera:
- De Caradenc
- Early Cherry
- Extra Early Cherry
- Myrobalan
- Paragon

Prunus angustifolia var. *varians* Wight and Hedr.:
- Eagle
- McCartney

Prunus orthosepala Koehne:
- *Prunus orthosepala*

Prunus subcordata Benth.:
- Sierra

Prunus simonii:
- Simon

HYBRIDS OR SUPPOSED HYBRIDS

Supposed parentage [1]	*Variety*	*Supposed parentage*	*Variety*
S × Si	Alhambra	W × A	Kiowa
Mu × S	America	Si × S × C × Mu	La Crescent
S × ?	Apple	S × A	Loring Prize
C × S	Banana	S × ?	Los Gatos
S × Si	Bartlett	Si × S	Mammoth
S × ?	Beauty Junior	C × ?	Marianna
S × ?	Bilona	S × A	May Beauty
S × A × ?	Biola	S × Si	Maynard
I × S	Black Beauty	S × C	Methley
S × Mu?	Bruce	Mu × ?	Milton
S × A	Bursoto	(Si × S × C × Mu) × Na	Minnesota 109
S × Si × ?	Cazique	I × D	Miracle
Si × ?	Chalco	S × A	Monitor
B × A	Cheresoto	S × A	Mound
A × S	Choice	S × Ch	Mrs. Bruce
S × Si	Climax	S × (Mu × S)?	Munson
S × ?	Combination	? × Mu	Nona
I × D	Conquest	S × A	Omaha
A × Ma	Crimson Beauty	S × (Mu × S)	Opata
S × A × Si	Discovery	A × S	Patten's XX
S × Ch	Donley	(S × Si) × ?	Phoebe
(Mu × S) × S	Duarte	(S × Si) × ?	Prize
S × Si × ?	El Dorado	H × A	Reagen
S × A	Eliott	S × Ch	Red Ball
?	Elsie	S × A	Red Wing
S × A	Emerald	H Mi × *P. cerasus*	Roadside
S? × D	Endicott	?	Russian hybrid
B × Na	Epoch	S × ?	Sacramento
B × S	Etopa	B × A	Sansoto
S × Mu	Excelsior	B × S	Sapa
B × S	Ezapatan	Si × S × C × Mu	Shiro
S × ?	First	S × An V	Six Weeks
S × A	Flichinger	S × ?	Solano
S × ?	Formosa	Sp × D	P. I. 32671
S × ?	Funk	Sp × D	P. I. 32673
S × A × ?	Gaviota	S × A	Stella
(Mu × S) × ?	Gee Whiz Plumcot	S × Ch	Sweetheart
A × Si × S	Gigantic	S × (S × Si)	Tanwick
Ma × Si × A × N	Glow	S × Mu	Terrell
S × Mu	Golden	A × ?	Theo. Williams
S × Na	Gonzales	S × ?	Thunder Cloud
H Mi × A	Hammer	A × Si	Toka
A × Si	Hanska	Si × A	Tokata
S × ?	Happiness	S × A	Tonka
S × hybrid	Howe	Si × S × C × Mu	Underwood
S × hybrid	Howe	S × ?	Upright
S × A	Hoyt	S × C	Vesuvius
S × Si × ?	Inca	B × S	Wachampa
A × S	Inkpa	S × A	Waneta
S × Ch	Jewell Carpenter	S × H	Waugh
Mu × S	Juicy	S × Si	Wickson
S × ?	June Twenty-fourth	D × S	Wilma
A × Si	Kaga	S × A	Winona
A × N	Kahinta	S × ?	Zulu

MISCELLANEOUS SPECIES, NO NAMED VARIETIES

Prunus alleghaniensis | *P. davidiana* | *P. mexicana*
P. besseyi | *P. fremonti* | *P. mira*

[1] Key to species of parents:
A = *Prunus americana*
An V = *P. angustifolia* var. *varians*
B = *P. besseyi*
C = *P. cerasifera*
Ch = Chickasaw plum
D = *P. domestica*
H = *P. hortulana*
H Mi = *P. hortulana* var. *mineri*
I = *P. insititia*
Ma = *P. maritima*
Mu = *P. munsoniana*
N = *P. nigra*
Na = Native plum
S = *P. salicina*
Si = *P. simonii*
Sp = *P. spinosa*
W = *P. watsoni*
? = Species unknown

CHERRIES

THE CHERRY is another very important stone fruit, although it is not grown so extensively in the United States as the peach and the plum. The varieties in which we are interested for their value as edible fruit belong to two groups, the sweet and the sour. Varieties of the former

Figure 15.—Eight-year-old trees of Napoleon sweet cherry (*Prunus avium*).

group are used principally for fresh-fruit dessert, while those of the latter make up the great bulk of the frozen and canned cherries of commerce for use in bakeries, restaurants, and homes for pies, preserves, and sauce. In fact, so important is their use for pies that this group of sour varieties is frequently referred to as pie cherries.

Unfortunately, our present-day cherry varieties are not so widely adapted over this country as we should like to have them. While the sweet cherry trees are as hardy in wood as the peach, they do not recover so well from winter injury. They blossom early in the spring, and the flowers are very susceptible to cold and frost injury. The sour cherry tree is as hardy as some apple varieties, but its blossoms are also quite tender to cold, and crops are frequently lost by spring frosts. In more southern latitudes in this country the trees do not thrive in the hot, dry summers, and in the more humid regions the fruits are very susceptible to brown rot. Chiefly because of special climatic requirements, the principal commercial production of sour cherries is limited to districts along the Great Lakes in the East, and of the sweet cherry varieties to the Pacific and Intermountain States of the West.

Classification of Cherries

All varieties of cultivated cherry belong to two species (*3, 18*). The sweet cherries, *Prunus avium* L., (fig. 15) are tall trees with few or no suckers from the roots and with leaves downy on the under side. The sour cherries, *Prunus cerasus* L., (figs. 16 and 17) are small trees with many suckers from the roots and with fruit sour to bitter in taste.

Figure 16.—Six-year-old trees of the Montmorency variety of sour cherry (*Prunus cerasus*).

Wild forms of the sweet cherry found growing in this country and in Europe are also called mazzard, bird, and wild sweet cherry. Some of these have escaped from cultivation.

The native habitat of the sweet cherry species is in southern and central Europe and Asia Minor. This species has been divided by botanists into different groups, but because of hybridization among the varieties it is rather difficult in many cases to classify them. Sweet cherries with soft, tender flesh form one group, known by pomologists under the French group name guigne or the English gean. These are also known as the heart cherries. These sweet, soft-fruited cherries may again be divided into dark-colored varieties with reddish juice, and light-colored varieties with colorless juice. Among the light-colored gean varieties are Coe, Ida, Elton, and Wood. Dark-colored ones are represented by Black Tartarian (fig. 18) and Early Purple The second group is distinguished by the firm, crisp flesh of the fruits and is referred to as the bigarreaus. Windsor, Republican, Bing, and Lambert are representative varieties of the black type, while light types are Yellow Spanish and Napoleon (fig. 15).

The native habitat of *Prunus cerasus* seems to be close to that of *P. avium* in the region about the Caspian Sea to western Anatolia. De Candolle concludes that *P. avium* extended westward more rapidly and was the first to become naturalized. Like the sweet cherry, the sour cherry is also divided into groups based on the color of the juice. Cherries with colorless juice are the amarelles, consisting of pale-red to red fruits more or less flattened at the ends (fig. 19). Common

Figure 17.—Mature trees of Montmorency cherry in bloom. This is the important sour cherry of commerce grown in the United States.

representatives of this group are Early Richmond and Montmorency (figs. 16 and 17). The second group called the morellos, contains varieties with very dark round to oval fruits and flesh with reddish juice. Typical varieties of this group are English Morello, Ostheim, and Olivet. A third type in the species is the marasca cherry, from which is made maraschino, a liqueur used in Europe and the United States in the manufacture of maraschino cherries. The marasca cherry is a native of the Province of Dalmatia, Yugoslavia, where the trees grow wild. The fruits of the marasca varieties are much smaller and darker and somewhat more acid than the common sour cherry. In the United States at the present time some varieties of sweet cherry such as Napoleon, and some sour varieties, are being used for making maraschino cherries.

The duke cherries (fig. 20) are intermediate in type and have sometimes been referred to *Prunus avium*, but more recently have been considered to be hybrids between *P. avium* and *P. cerasus*. In France they are called royals. May Duke, perhaps one of the oldest varieties grown in the United States, Reine Hortense, and Late Duke are important varieties of this group. In the duke cherries

many characteristics of fruit, skin, flesh, juice color, and flavor, as well as of tree growth, are intermediate between the sweets and sours.

Three other species of cherry that have been used by breeders are the Nanking or bush cherry, *Prunus tomentosa* Thunb , an inhabitant of central Asia; the sand cherry, *P pumila* L , of the shores and

Figure 18.—Sweet cherries are more or less heart-shaped and are sometimes referred to as heart cherries. Black Tartarian, shown above, is a variety of the gean type with dark flesh and reddish juice. The bigarreau type is similar in appearance but has firm flesh.

beaches of the eastern United States; and the western sand cherry or Bessey cherry, *P. besseyi* Bailey, of the western United States.

In addition to the wild sweet or mazzard cherry, two other species are important from the standpoint of stocks on which to bud or graft varieties for propagation. These are the small wild, inedible sour cherry of southern Europe, *Prunus mahaleb* L , known as the mahaleb cherry, and the small wild red or pin cherry of the Northern States and Canada, *P. pensylvanica* L. f.

Attempts have also been made to locate pleasant-flavored strains of the chokecherry, *Prunus virginiana* L. Some strains are quite inedible until fully ripe.

Objectives in Cherry Breeding

One of the main objectives in cherry breeding is the production of high-quality sweet varieties that will prove more hardy in tree and blossom characters than many of those now available for planting. The production of such a delicious fruit as the sweet cherry is now

limited to a very few regions of this country. Even in those regions where it can be grown there is need for firm-fleshed varieties that do not crack and that will ripen over a long season. At the present time we have no firm-fleshed early-ripening varieties of the bigarreau type. The unsatisfactory viability and germination of seed of early-ripening varieties impede progress in this direction at the present time.

In obtaining varieties that will be suited to regions where moderately low winter temperatures prevail, the matter of understocks may be of first importance. The chief limiting factor in growing hardy cherries

Figure 19.—Sour cherries of the amarelle group, including pale red to red types with colorless juice: *A*, Early Richmond; *B*, Saint Medard.

in the northern Great Plains area, as well as in certain other parts of the United States, is the relative tenderness of some mahaleb and mazzard stocks used in propagation. Selection of better understocks that will prove more cold-resistant and more widely adapted than those in present use is worthy of further investigation. Selections of native cherries that appear to be better adapted to various soil and climatic conditions, such as hardier strains of our native mazzard and mahaleb stocks, may prove fruitful of results (*21*). Cherries are not grown at the present time in the vast area comprising the southern part of the United States, principally because of the susceptibility of our available varieties to certain diseases. There is need for the development of disease-resistant varieties for this region.

More genetic and cytological studies are needed, particularly of hybrids between the sweet and sour varieties, as a basis for more intelligent choice of desirable parents. Some of the duke varieties

are very excellent cherries but they are not highly productive. Methods of inducing polyploidy in order to obtain greater fertility in cherries has received little attention.

Methods of Cherry Breeding

The methods used in breeding new varieties of cherry are not different from those already discussed for the peach and the plum. Since all of the important varieties of *Prunus avium* have been shown to be self-unfruitful (*28, 30*) emasculation is unnecessary, but with the sour and duke varieties the blossoms must be emasculated.

Figure 20.—Eight-year-old trees of the May Duke variety of the duke group of cherries

One of the important problems confronting the cherry breeder at present is to find methods for growing the seeds of early-ripening varieties.

Improvement in Varieties

Breeding of new varieties of cherries does not seem to have attracted the interest of private breeders to the extent noted with peaches and plums. Interest has always been maintained in a search for new varieties, but progress in obtaining them has been slow. The failure to develop new varieties may be due partly to the fact that the cherry is not at home over such a large area of this country as the peach and the plum. The tenderness of the sweet cherry (*Prunus avium*) varieties, with the resulting loss of trees during cold winters, has largely limited their culture to the more protected areas along the Great Lakes and to the Pacific and Intermountain States of the West. The failure to obtain new varieties, particularly the sweet sorts, may also be due to the failure of the seed to grow.

The success obtained by two private breeders is worthy of mention. The pioneer breeding work of the brothers Henderson and Seth Lewelling in Oregon dates back to 1848 (*18*). In that year Henderson Lewelling carried an assortment of varieties of peach, apple, pear, plum, and cherry by wagon from Iowa to Oregon. These were planted in Milwaukie, Oreg., as a source of material for nursery and variety-improvement work. One of the most important varieties of cherry in this collection was the Napoleon. Apparently the tag had been lost, and the variety was renamed the Royal Ann, the name by which it is known in the Pacific Coast States today. From this stock of Royal Ann and other cherries, three important new varieties of the black bigarreau type were developed, Republican, Lambert, and Bing. Republican, possibly a cross of Napoleon and Black Tartarian, originated as a seedling in Seth Lewelling's orchard in 1860. Lambert originated as a seedling under a tree of Napoleon planted by Lewelling in 1848. From a seed of Napoleon planted in 1875 in Milwaukie, Seth Lewelling grew the promising seedling that later he called Bing. These excellent varieties developed by the Lewelling brothers laid the foundation for the present cherry industry in the Pacific Northwest as well as in California. The Bing, Lambert, Republican, and Napoleon are at the present time the leading commercial varieties of sweet cherry in this region.

At about the time that the Lewellings were working on the development of cherry varieties in Oregon, P. J. Kirkland, of Cleveland, Ohio, was engaged in similar work for the eastern United States. Varieties introduced by Kirkland that have been grown and are still being grown to some extent are the soft-fleshed sweet varieties Black Hawk, Kirkland, and Rockport.

In view of the results obtained by these men it is rather surprising that no enterprising breeder has become interested in more recent times in searching for better varieties and types of sweet cherries adapted to this country.

Cherry Breeding in the United States

The New York (State) Agricultural Experiment Station at Geneva has done the most work on cherry breeding in recent years. The first crosses were made in 1911. To date, about 1,200 seedlings have been planted for fruiting, and in addition there are a few hundred in the nursery for future planting. Sixty-two different sweet, sour, and duke varieties and a few seedlings have been used in the breeding studies. The varieties used most extensively were Abesse d'Oignies 33 times, Abundance 47, Bing 57, Burbank 9, Coe 16, Early Rivers 35, Early Purple 9, English Morello 46, Elton 41, Emperor Francis 45, Early Richmond 21, Giant 82, Gil Peck 15, Hedelfingen (*Géante d'Hedelfingen*) 27, Ida 12, Kirtland 50, Knight 10, Ludwig 27, Lambert 81, Lyons 58, May Duke 72, Montmorency 73, Napoleon 103, Ostheim 26, Olivet 14, Oswego 11, Reine Hortense 25, Royal Duke 9, Republican 32, Schrecken 30, Seneca 74, Schmidt 74, Windsor 59, Wood 24, and Yellow Spanish 54.

Unfortunately, many cherry seeds failed to germinate, and consequently from thousands of seeds comparatively few trees were obtained.

The seeds of early varieties were nearly 100 percent nonviable. The Seneca, a very early black sweet cherry, was produced at the Geneva station by crossing an early unknown sweet with the Early Purple. This variety originated in 1911 and was sent out for trial in 1924. The only other seedling that has been named was derived from a cross made in 1925 between Napoleon and Giant. This seedling was named Gil Peck upon request of the Indian tribes of New York, who were very fond of the late Gilbert W. Peck, a Cornell extension worker in pomology. The Gil Peck was introduced in 1926.

The objectives of the work in New York have been the production of firm-flesh sweet cherries that do not crack or rot and that ripen from early to late season. To secure lateness, large-fruited varieties were crossed with Abundance and with a small, very late, firm-flesh cherry called Oswego. Late-blooming mazzards have also been used in order to secure later blooming varieties that may escape late spring freezes.

In addition to fruit of good quality for commercial purposes, productive hardy trees have been given consideration in this work. Little work has been done with the sour (*Prunus cerasus*) group of cherry, because the present commercial varieties, Montmorency and Early Richmond, have been found fairly satisfactory for New York. The production of desirable duke cherries has also been given consideration, inasmuch as a productive high-quality duke would doubtless meet with favor among cherry producers and consumers.

In South Dakota, N. E. Hansen has been actively engaged since 1900 in breeding cherries suited to the west north central States. He has made many crosses, using the western sand cherry, *Prunus besseyi*, and other species of *Prunus*. The sweet cherries, *P. avium*, which are raised in the Eastern States and so extensively on the Pacific coast, are not hardy in the northern prairie States. The sour cherries, *P. cerasus*, are much hardier than the sweets, but they are not generally planted in this region. The Early Richmond and some other sour varieties are grown to a limited extent in the southern part of the State. Attempts to hybridize sweet and sour varieties with the native cherries have not been successful.

The following have been developed and introduced:

Select South Dakota sand cherries (*Prunus besseyi*): Sioux, Tomahawk, and S. Dak. No. 5.

Sand cherry × Japanese plum: Sapa, Wachampa, Etopa, Eyami, Enopa, Ezaptan (sand cherry × Burbank Sultan plum), Opata, Owanka, Okiya, Cikana (sand cherry × Gold plum), Skuya, Wohanka, Wakapa (probably sand cherry × unknown Japanese plum).

Sand cherry × native plum: Cheresoto, Sansoto (sand cherry × De Soto plum).

Sand cherry × plum: Champa (sand cherry hybrid, a seedling of Sioux open-pollinated), Oka (seedling of Champa open-pollinated, probably with Japanese plum).

Sand cherry × Purple-leaf Persian plum: Stanapa (purple-leaved, semi-dwarf), Cistena (purple-leaved, dwarf).

Sand cherry × European apricot: Yuksa (sand cherry × New Large apricot).

At the Iowa Agricultural Experiment Station cherry-breeding work is being carried on by utilizing greenhouse-grown trees in the same way as in the work at this station with plums and peaches. The varieties consist of six species of *Prunus*, namely, *avium*, *cerasus*,

besseyi, japonica Thunb., *tomentosa,* and *capuli* Cav. Trees of the following crosses are being grown in the nursery: Sapa plum (*P. salicina* Lindl. × *P. besseyi*) × Gold cherry (*P. avium*); *P. serotina* Ehrh. × *P. capuli,* and Zumbra × *P. tomentosa.* The object of this work is to obtain varieties of cherry hardy for Iowa and suitable for the Great Plains region.

At the North Dakota Agricultural Experiment Station, work on cherry breeding is carried on with objectives similar to those in South Dakota and Iowa. The Cooper sand cherry hybrid was introduced in 1935. Because of good quality of fruit and hardiness of tree, it is considered a substitute for the sweet cherry in that State.

In past years about 400 seedlings of open-pollinated Compass cherry have been grown. Only one seedling had horticultural value. About 500 chokecherry selections have been grown, and from this work variety improvement seems possible from the use of these cherries as parents. Fifty F_1 seedlings were obtained from crosses made in 1926 of chokecherry × *P. maackii* Rupr. These seedlings are also of genetic interest and are under study. Seedlings of hardy Russian sorts and of open-pollinated Anoka are also being grown.

At the United States Northern Great Plains Field Station at Mandan, N. Dak., sour and sweet varieties of cherries have been crossed with pin cherries (*Prunus pensylvanica*), western sand cherries (*P. besseyi*), Nanking cherries (*P. tomentosa*), and chokecherries. Seeds have been produced, but in most cases they failed to grow. One tree, a cross between Wragg and pin cherry, seems to be fairly drought-resistant and hardy. It blooms profusely but does not set fruit, probably because of self-unfruitfulness.

Several hundred pin cherry seedlings have borne fruit, but none has been good enough to select.

Several thousand western sand cherry seedlings have been grown. This hardy native fruit shows a decided and varied response to cultivation; there are marked variations in habit of growth and in size and quality of the fruit. A number of promising selections have been made and propagated for further testing. This fruit has also been used in crossing with plums and Nanking cherries. Some of the latter crosses are bearing, and both fruit and bush characteristics are intermediate between the western sand cherry and the Nanking cherry. Second-generation seedlings have been grown.

Large numbers of chokecherry seedlings have been grown, and while they show considerable variation, no real "chokeless" seedling, i. e., entirely nonastringent, has been found. A few of the best have been propagated on *Prunus maackii* stock for further testing.

Thousands of seedlings of the Nanking cherry have been fruited in the testing blocks. This fruit is not entirely hardy and tends to be a shy bearer. It has been used in crossing with standard varieties of cherries, the western sand cherry, and plums. The only viable seeds obtained were from the western sand cherry crosses.

In addition to the breeding work at the various institutions, extensive variety collections are located in a number of States where breeding material may be obtained. Some of these are the New York (State) Agricultural Experiment Station, the Ohio Agricultural Experi-

ment Station at Wooster, the Colorado State College at Fort Collins, the Utah Agricultural Experiment Station at Ogden, the California Agricultural Experiment Station at Davis, and the Oregon Agricultural Experiment Station at Corvallis.

Cherry Breeding in Canada

Cherry-breeding work at the Horticultural Experiment Station at Vineland, Ontario, Canada, was begun in 1915 and has been continued up to the present time. During the period 1915 to 1935, 2,587 seedlings were obtained and planted for study. These seedlings were from 27 variety crssoes and 27 open pollinations. Sixteen have been selected as having horticultural value. Two hundred and eighty-one seedlings were obtained from crosses made in 1931, using Bing as the seed parent and Black Tartarian, Napoleon, and Victor as pollen parents, to obtain large, nonsplitting, black varieties. From crosses made in 1935, 1,040 seedlings have been obtained from Hedelfingen as seed parent and Black Tartarian, Bing, Victor, and Windsor as pollen parents, with the same object in view.

From the early cherry-breeding work the Victor variety was introduced in 1935. This variety was a selection from seed of open-pollinated Windsor, which was collected in 1916 by F. S. Reeves. It is a large, attractive white cherry. Approximately 4,000 trees of this variety have been planted in southern Ontario.

Self-Fertility in Cherry Varieties

Gardner (*14*), in 1911, working in Oregon, failed to get a set of fruit from selfing 11 varieties of sweet cherry. In 1912 he attempted to intercross Bing, Lambert, and Napoleon. These varieties proved to be not only self-incompatible, but incompatible with each other, that is, they would not set fruit when selfed or when cross-pollinated among themselves. In orchards where Napoleon was interplanted with Republican, and away from the influence of other varieties, the Napoleon set a full crop. The same was true where Lambert and Bing were interplanted with Black Tartarian.

The results of early cherry pollination work from 1911 to 1913 in Oregon, as well as later work in that State and in California, show that all varieties of sweet cherry tested were self-incompatible. Republican, Black Tartarian, Coe, Early Purple, Elton, Knight, Major, Francis, May Duke, Rockport, Waterhouse, Willamette, Windsor, and Wood were all self-incompatible. Republican and Black Tartarian were found to be good pollinizers for all the varieties. They, of course, do not set fruit when selfed.

Crane and Lawrence, working in England, have tested 33 varieties and found all of them to be self-incompatible. Important self- and cross-incompatible varieties were Black Eagle, Early Rivers, Knight (Knight's Early Black), and Bedford Prolific, while among cross-compatible varieties were Black Tartarian, Schmidt, Wood, and Windsor.

For all practical purposes, therefore, we must consider all true sweet-cherry varieties of *Prunus avium* to be self-unfruitful, that is,

no fruit will set from blossoms pollinated with their own pollen, since fertilization will not take place. The genetic explanation of self-incompatibility of style and pollen and its relation to failure of fruit to set has already been discussed in the section on plums.

Types of Sterility

Nearly all of the varieties of sweet cherries fail to set fruit when the flowers are pollinated with their own pollen. They are therefore said to be self-sterile. However, the pollen grains and egg cells of these varieties are functional, for the pollen will grow when placed on the stigma of another variety, and in like manner the egg cell will develop if fertilized with pollen of another variety. With most of the stone fruits fertilization is required before the fruit will develop, and a variety that does not set fruit because of the failure of its own pollen to effect fertilization of the flowers is said to be self-unfruitful.

Strictly speaking, sterility may be due to three causes (*23*): (1) Flowers may be sterile because of their morphological development. Failure of the anthers or pistils, or both, to develop, and failure to develop viable pollen or functional egg cells, may result in nonfruitfulness. It is recognized that such situations may be due to genetic causes. (2) Sterility may also be physiological. The pollen grains and egg cells may be normal; fertilization is effected, but the embryo does not grow because of certain nutritional disturbances. (3) Sterility may be due to incompatibility. In this case the pollen grains are normal and will develop in the style of other varieties and bring about fertilization of the ovules, but they will not function in the style of the flower of the same variety. It is this latter type of sterility that is most frequently encountered in the stone fruits. Nearly all of the sweet cherry varieties are self-unfruitful because of incompatibility. Varieties such as Napoleon, Windsor, and Black Tartarian will not set fruit when the flowers of any one of them are pollinated with its own pollen. If, however, Black Tartarian pollen is applied to Napoleon or Windsor, a large percentage of the flowers will set fruit. Likewise, if Windsor pollen is applied to Napoleon or Black Tartarian, fruit-setting will occur.

The genetic basis of incompatibility has already been discussed in the section under plums.

Genetic and Cytological Studies With Cherries [10]

In contrast to the sweet cherries, varieties of sour cherries are self-fertile, and the pollen of sour varieties will also effectively cause fruit-setting on sweets.

In duke cherries varying degrees of self-compatibility occur. Crane and Lawrence (*10*), working in England at the John Innes Horticultural Institution, have obtained the following percentage of set from selfing important duke varieties: 9 percent for Late Duke, 3 percent for Empress Eugenie, 1 percent for May Duke. Reine Hortense set no fruit. The results obtained from cross-pollinations between sweet,

[10] This section is written primarily for students or others professionally interested in genetics or breeding.

sour, and duke cherries have varied considerably. According to Crane and. Lawrence, sweet varieties pollinated by sour varieties generally produce and mature fruits freely, but from reciprocal pollinations fruits are less freely formed. In a similar way fruit production is less when the dukes are pollinated by sweet varieties than when reciprocal pollinations are made.

We have little knowledge about the origin of our present cherry varieties. Three varieties produced by Thomas Andrew Knight, resulting from a cross of a sweet (bigarreau) × May Duke, were Waterloo, Knight (Knight's Early Black), and Black Eagle, and the latter two would pass for sweet cherries. In pollination studies to determine the incompatibility of varieties, it has been observed, both in this country and in England, that individuals of the same variety appear to differ in their pollination requirements, and it is possible that distinct strains of such varieties or types as Black Tartarian or Napoleon have been propagated. Because of the fact that all varieties of *Prunus avium* are self-unfruitful it has been impossible to raise selfed progeny to study the inheritance of characters and determine genetic relationships. In studies made at the John Innes Horticultural Institution in England, Crane observed that in selfed families raised from varieties of *P. cerasus*, seedlings with *P. avium* characters frequently appeared, and in families raised from crosses between varieties of *P. avium*, occasional seedlings occurred which showed marked *P. cerasus* characters. Furthermore, seedlings in families raised from *P. avium* × *cerasus* resembled the dukes in many characters but not in all.

Cytological investigations of the cherries show the somatic chromosome number ($2n$) in *P. avium* to be 16, and it is apparently diploid. In *P. cerasus* and the dukes the number is 32. Darlington (*11*), who has studied the chromosome behavior in a number of cultivated varieties of cherry, considers that *P. cerasus* is a true tetraploid, not derived simply from *P. avium*, but one possessing additional elements probably derived from *P. fruticosa* Pall., another tetraploid. All of the sweet cherries examined by Darlington had extra chromosomes beyond the diploid number. Irregularities occur in chromosome pairing, but it does not appear that there is any correlation between the actual chromosome number and the incompatibilities observed in sweet cherry varieties. Selfed seedlings of sour and duke varieties showed a chromosome number of 32. In crosses between the sour and dukes an examination of the progeny shows that the chromosome number is also 32. However, in crosses between dukes and sweets, and sours and sweets, the progeny showed the intermediate number 24 in some cases, as we might expect, and in others 32. The cultivated duke varieties appear to be tetraploids that have arisen from hybridization between the diploid sweet cherries and the tetraploid sours. In experimental studies, however, crosses between some tetraploid sours and diploid sweets have yielded seedlings with 24 chromosomes that presumably were triploids and proved to be highly sterile.

B. R. Nebel, at the New York Agricultural Experiment Station, has been studying the cytology of interspecific hybrids. From crosses

between sour and sweet cherries, 22 triploid first-generation trees have been obtained, and these are fruiting on the station grounds. In attempting to backcross from these hybrids only 1 fruit was obtained in 700 pollinations. Open-pollinated seed was then used, and this gave nearly 50 second-generation seedlings. Upon cytological examination of this second-generation material there appeared to be a gradation downward in chromosome numbers through loss of some of the supernumerary chromosomes of the sour species. It is possible that the second-generation seedlings will be more fertile than the first-generation, and that backcrosses with firm-fleshed sweet cherries will give diploid dukes that are interfertile with sweet cherries. As already mentioned, if autopolyploidy could be induced, the first-generation triploids could be made fertile directly and much time could be saved.

Crane and Lawrence report from their studies of the inheritance of flesh color in sweet cherries that white is recessive to black. In crosses between white varieties only white was obtained. Bigarreau du Schrechen is considered homozygous for black, since in all crosses where this variety was used as a parent all of the progeny produce black fruits. Other black varieties, such as Early Rivers, Bedford Prolific, Black Tartarian types A and B, Late Black, and Schmidt, are heterozygous for flesh color. It appears, however, that when the different shades of fruit color are considered, ranging from dark to white, through various pinks and reds, a number of genes may be involved in color inheritance.

Selfed sour cherry (morello) varieties with roundish oblate fruit gave seedlings that yielded occasional long fruits. Kentish Red, a variety with roundish oblate fruits, gave a progeny that yielded fruits of variable size and shape.

Appendix (Cherry)

Table 8.—*Locations of cherry-breeding work and names of workers in the United States and Canada*

State or country, institution and location	Early workers	Workers actively engaged at present
California:		
Agricultural Experiment Station, Davis.	A. A. Hendrickson, W. P. Tufts, G. L. Philp.	W. P. Tufts, G. L. Philp, E. C. Hughes.
Iowa:		
Agricultural Experiment Station, Ames.	S. A. Beach	T. J. Maney.
New York:		
Agricultural Experiment Station, Geneva.	S. A. Beach	U. P. Hedrick, R. Wellington, G. H. Howe, B. R. Nebel.
North Dakota:		
United States Northern Great Plains Field Station, Mandan.	Max Pfaender	W. P. Baird.
Agricultural Experiment Station, Fargo.		A. F. Yeager.
South Dakota:		
Agricultural Experiment Station, Brookings.	N. E. Hansen	N. E. Hansen.
Utah:		
Agricultural Experiment Station, Logan.		F. M. Coe
Canada:		
Horticultural Experiment Station, Vineland, Ontario.		F. E. Palmer, G. H. Dickson.

Cherry Material at the California Agricultural Experiment Station, Davis, Calif.[11]

Prunus tomentosa:
- Var. Bush Cherry (P. I. 36086)

P. pseudocerasus:
- Var. Tangsi (P. I. 18587). (Season very early.)

P. avium:
- Abundance
- Allen
- Bassford
- Bauman May
- Bedford Prolific
- Belle de Drureo
- Belle d'Orleans
- Best
- Biggareau Blanc d' Espagne
- Bigarreau d'Italie
- Bing
- Black Oregon
- Black Republican
- Black Sweet
- Black Tartarian
- Bohemian
- Burbank
- Burr's Seedling
- Bush Tartarian
- California Advance
- Centennial
- Chapman
- Cleveland
- Coop's Special
- Deacon
- Dikeman
- Dr. Flynn
- Double White
- Downer
- Dyehouse
- Early Purple Guigne
- Early Rivers

P. avium—Continued.
- Elton
- Emperor Francis
- Garrafal
- Garrafal le Grand (P. I. 33223)
- Giant
- Gold
- Hedelfingen
- Hinton
- Hoskins
- Improved Black Tartarian
- Jaboulay
- Knight
- Koontz Mammoth
- La Cima
- Lamaurie
- Lambert
- Late Bing
- Lewelling
- Long Stem Royal Ann
- Long Stemmed Waterhouse
- Major Francis
- Mezel
- Napoleon
- Ord
- Ostheimer Weichsel
- Oxheart
- Paul
- Pontiac
- Porter's Tartarian
- Ramon Oliva
- Roe
- Royal Stewart
- Saylor
- Schmidt
- Seneca
- Sharp

P. avium—Continued.
- Shelton
- Negro de la Rivera (P. I. 73456)
- Risada de Kenter (P. I. 73457)
- Thompson
- Transcendens Black Heart
- Vaughn
- Waterloo Heart
- White Carron
- Willamette
- Windsor
- Wood

P. cerasus:
- Baldwin
- Dyehouse
- Early Richmond
- English Morello
- Homer
- Large Montmorency
- Montmorency
- Nelson
- Terry
- Vladimir
- Wragg

Dukes:
- Empress Eugenie
- Late Duke
- May Duke
- Minehin
- Noble
- Olivet
- Reine Hortense
- Royal Duke

Hybrids:
- New Century. Parentage, *P. cerasus* × (*P. avium* × *cerasus*).

Cherry Varieties at the New York Agricultural Experiment Station, Geneva, N. Y.

- Abbesse d'Oignies
- Belle di Barbanti (U. S. D. A.)
- Bianco Rosatio di Piemonte (U. S. D. A.)
- Bicentenaria (U. S. D. A.)
- Bigarreau de Schrecken
- Emperor Francis
- Garrafal le Grand
- Geante d'Hedelfingen (Germany). (Synonym of Hedelfingen.)
- Giant
- Gil Peck
- Grosse Lange Lothkirsche (Germany). (Synonym of English Morello.)
- Ludwig Bigarreau
- Marasca di Verona (U. S. D. A.)
- Marasca Moscata (U. S. D. A.)
- Nero Grossa di Pimento (U. S. D. A.)
- Noir de Guben
- Seneca

[11] This list contains, besides well-known varieties, local selections and other sorts the names of which cannot well be made at this time to conform to the code of nomenclature.

APRICOTS

The apricot is prized by all who like the stone fruits, and when eaten fresh it is considered by many to be the most delectable of this group. Unfortunately, however, very few apricots are grown for fresh fruit in the States east of the Rocky Mountains, and most people know the flavor of this fruit only from the canned or dried product. Its production is restricted to a relatively small area in this country where climatic conditions are favorable. Most varieties can withstand winter cold as well as peaches, but the blossom buds develop rapidly under favorable growing temperatures in late winter after the rest period is over, and the crops are frequently lost from late freezes and spring frosts.

The commercial production of the apricot (fig. 21) is confined largely to the Pacific Coast and Intermountain States (*5*, *20*). California leads with a potential average production considerably in excess of 200,000 tons. Of the average crop of 266,000 tons harvested during the years 1931–33, approximately 76 percent was dried, slightly over 14 percent canned, and about 10 percent was shipped or consumed locally as fresh fruit. Because of the great perishability of this fruit and the need for quick handling, fresh apricots are on the market in the Eastern States for only a short time and their distribution is limited to large centers of population.

Botany and History of the Apricot

All of the important commercial varieties of apricot grown in this country today belong to the species *Prunus armeniaca* L. The name of the species, like that of the peach, is a geographical misnomer. The apricot was formerly considered a native of the Caucasus and Armenia, but later studies suggest that China is its native home. It is said that Alexander the Great brought the apricot from Armenia to Greece, whence it was taken to Italy. The Romans cultivated this fruit, and it is described in the writings of Pliny and Dioscorides. It was later carried to France, and there is mention of its being in England in Turner's Herbal, published in 1562. The fruit is now cultivated in all of central and southeastern Asia, and in parts of southern Europe and northern Africa. There seems to be no mention of it in the United States until 1720, when it was said to be growing abundantly in Virginia. It was doubtless among the fruits brought into southern California early in the eighteenth century by the Mission Fathers. Its culture spread to the valleys farther north, where climatic conditions were more congenial. Wickson (*33*) reports that Vancouver found a fine orchard of fruits, including apricot, at Santa Clara in 1792. In 1935, 17 varieties were described as growing in England. Downing (*12, pp. 236–242*) names 26 varieties, and the American Pomological Society (*1*) lists 11 varieties as growing in the United States in 1879.

In tree, fruit, and flower characters the apricot seems to be somewhat intermediate between the plum and the peach. The trees are large and spreading, and in this respect are more like the peach and some of the Japanese plums. The leaves are broad, heart-shaped, dark green in color, and held erect on the twigs. The flowers are

white, resembling those of the plum in color, but are borne not in clusters but singly or doubly at a node on very short stems. Like the peach, the apricot is self-fruitful and will set fruit when its blossoms are selfed. The pit is smooth, somewhat like that of the plum, but broader, somewhat flatter, and more winged. The fruit is nearly smooth, round to oblong, in some varieties somewhat flattened, and in general rather more like the peach in shape. The flesh is typically

Figure 21.—Peach and apricot growing constitutes an important industry in California. The apricot trees, in the immediate foreground, and the peach trees in the rear are a part of a large orchard with rows 3 miles long.

an attractive yellow to yellowish orange. The kernels of some varieties are sweet.

The peach, plum, and apricot may be readily intergrafted. The apricot does well on peach stock, but the peach on apricot stock is not entirely satisfactory.

In addition to the common apricot (*Prunus armeniaca*), which comprises all of the commercial varieties grown in this country, several other species are of interest to the breeder. The black apricot (*P. dasycarpa* Ehrh.) has fruits of small size, dark purple or black in color, and for the most part of inferior quality. The trees more closely resemble the plum and possess considerable hardiness in wood and bud.

The Japanese apricot (*P. mume* Sieb. and Zucc.) is noted principally for the ornamental character of the trees. The flowers and fruits also are very attractive.

Types native in other countries have been described as species but are classed by some authorities as subspecies. The Russian apricot (*P. sibirica* L.), is possibly a strain of the common apricot (*P. armeni-

aca). Trees of the Russian apricot differ from the common apricot in bearing smaller fruit of poorer quality. They are considered very much hardier in their native home, but certain strains brought into this country have not shown superior hardiness under test. The trees have a characteristic upright growth habit, are thickly branched, and possess more thornlike spurs. The small fruits set in clusters.

Another probable subspecies, the Manchurian apricot (*P. mandschurica* Koehne), is a common wild tree in central Chosen. Its fruit is similar to that of the common apricot, but the leaves differ, and its bark is thick and corky. This subspecies may be a selected strain of the common apricot.

The apricot is widely distributed throughout Asia, and a large number of seedlings have been observed growing wild in various localities. In China some travelers report the apricot only as a cultivated tree, but others have found it growing wild in the northern Provinces.

Breeding Material

The apricot is less rich than some of the other stone fruits in species and horticultural varieties suitable for breeding material. The raw material consists of many old varieties introduced from England and France. Among those recognized as of English origin are Blenheim, Early Moorpark, Moorpark, and Hemskirke. These are all varieties, of high quality, with the Blenheim maintaining first importance as a commercial variety. Varieties of French origin are Peach, Oullins Early, Montgamet, Luizet, and Royal. Royal is the most important commercial variety of this group. Like the English varieties, all the French varieties have certain commercial limitations. There is an excellent opportunity for the apricot breeder to combine their desirable characters by cross breeding. Work of this kind is already under way at State and Federal agricultural experiment stations, as will be pointed out later.

A large number of varieties have been introduced from the Union of Soviet Socialist Republics, many of these by J. L. Budd, of Iowa. As a class they are more hardy in bud, later in blossoming, with fruit of smaller size and poorer quality, but they are very productive. Some of the more important varieties of this group are Alexander, Budd, Gibb, Shense (Acme), Superb, and Toyahvale. Little work has been done in combining the qualities of these hardy sorts, which some botanists consider a separate species (*Prunus sibirica*), with the commonly grown varieties from western Europe.

In the last half century a number of promising seedlings and strains of American origin have been selected, but only the Tilton ranks with the older European sorts as an important commercial variety. As might be expected, most of the American varieties originated in Pacific Coast States. Among the more important are Newcastle, Alameda Hemskirke, Routier Peach, Derby Royal, and Sparks Mammoth, from California. Other varieties of more recent origin are Wenatchee Moorpark, which has been reported to be similar to if not identical with Moorpark, Riland, Gilbert, and Sofia, originating in the State of Washington. Among other older American varieties are Early Golden and Superb.

The apricot has been crossed with varieties of plum, particularly the Japanese plum. Luther Burbank produced a number of seedlings by crossing the apricot with this plum. Some of the more promising of these have been introduced under the group name plumcot. Among the more important are Apex, Corona, Rutland, Silver, and Triumph.

The crosses of apricot with plum have apparently been more successful than those with peach. No horticulturally satisfactory peach-apricot varieties have been reported.

Objectives in Apricot Breeding

If apricot culture is to be extended beyond the present restricted areas where climatic conditions are favorable, varieties must be developed that are later in flowering in spring. From material that has been brought into this country, differences in bud hardiness and in blooming have been observed. There is need for the introduction of varieties from countries where apricots are growing and surviving temperatures as low as those obtaining during the winter months in this country. Many of these will doubtless prove worthless from the standpoint of edible fruit quality, but will serve as breeding material for the development of better varieties. In California considerable loss results from the dropping of blossom buds of certain varieties. Varieties that have a short rest period, are needed for those sections of the country where the winter temperatures are not low. Better canning, drying, and shipping varieties are also in demand. Evidence at hand would indicate that the commercial quality of varieties can be improved by breeding.

There is little information about the development of varieties by private breeders. A number of chance seedlings have been discovered by individuals, but it does not appear that any conscious attempt to select or breed new varieties has been carried on to the extent that it has with the other stone fruits. It is likely that many who were interested in better varieties were discouraged in their attempts because the parent material available for crossing was in itself not sufficiently hardy.

In the selection of material for breeding, difficulty may be encountered in establishing the trueness to name of varieties, since the same variety may be grown in two or more localities under different names. Some of the varieties representing desirable types are Moorpark, Royal, Blenheim, Tilton, Montgamet, and some selections of Russian and Japanese origin. For breeding studies in the eastern United States, where hardiness is an important factor, varieties should be used that have been tested and have demonstrated superior hardiness, such as strains of Russian varieties introduced by Budd, and more recent importations made by Hansen, of South Dakota, and the Division of Plant Exploration and Introduction, Bureau of Plant Industry, United States Department of Agriculture.

Apricot Breeding at State and Federal Stations

Apricot breeding was started at the New York (State) Agricultural Experiment Station in 1922. Eighteen varieties, one seedling, and two P. I. numbered seedlings have been used. Eighty-four seedlings derived from definite crosses, 1,424 from open cross-pollination, and 9

from self-pollination have been set in the orchard for fruiting. Varieties used most extensively have been Alexis 6 times, Doty (a local seedling) 15, Downing (late blooming) 5, Montgamet 6, Oullins Early 13, St. Ambrose 5, and Toyahvale 5. A seedling grown from a seed imported by the Department of Agriculture as P. I. 34265 has been considered worthy of a name. This variety was temporarily called "Frascati", as the seed was thought to have been imported from the vicinity of Frascati, Italy, but more recently it has been given the name Geneva.

At the North Dakota station apricot breeding work was started in 1924 in an attempt to develop varieties of sufficient hardiness to stand the winters of the northern Great Plains area. Over 2,000 seedlings are being grown and studied for their hardiness and quality of fruit.

At the South Dakota station, N. E. Hansen has been propagating trees from seeds collected by him in northern Manchuria in 1924. The fruits were taken from trees growing in localities reported to have minimum temperatures of $-47°$ F. Twenty-three selections, called the Manchu group, have been propagated for test. Additional collections made in 1934 in eastern Siberia for propagation at Brookings are expected to give seedlings with greater hardiness than the Manchu.

Breeding work at the California station at Davis, Calif., was started in 1930. The objective is the development of varieties of high quality suitable for shipping as fresh fruits, canning, and drying, but lacking some of the faults of the old varieties now grown commercially. Varieties used as pollen and seed parents have been Tilton, Royal, Hemskirke, Blenheim, St. Ambroise, Peach, Newcastle, Moorpark, Oullins Early, and in addition strains of Moorpark and Hemskirke. In the seasons of 1933 and 1934, one seedling each was obtained from the following interspecies crosses: Royal × *Prunus pseudocerasus*, *P. mume* × Royal, Pringle Late × Rutland plumcot, Diamond Jubilee nectarine × Royal, and Lovell peach × Royal. From the crosses made during 1930–35 there are at the present time over 2,000 seedlings growing in the orchard.

This material should provide a sufficiently large progeny for genetic studies of the varieties used as parents and serve as a source of superior seedlings that may be worthy of naming. A list of the crosses and the number of seedlings in each cross, as well as a list of varieties now being grown, is given in the appendix to this section.

At Palo Alto, Calif., apricot breeding by the United States Department of Agriculture in cooperation with Leland Stanford Junior University has been in progress since 1922. A search for varieties of high quality that would prove more satisfactory for the established apricot districts has been the main objective of this work. About 60 promising hybrids have been selected for further studying and testing. The more common varieties, such as Blenheim, Tilton, Moorpark, Royal, Newcastle, and Hemskirke, have been used as seed and pollen parents, and in addition the less common varieties Bergetti, Montgamet, McKinley, Luizet, Bremner, and Sparks. Hybrids of these varieties have been recrossed, and other combinations have been made by using promising parents introduced from southern Europe, Africa, and Asia in an effort to obtain certain desirable characteristics in the

progeny. In this material from abroad are included Giallo di Tortona, Tunis seedlings, Japanese seedling 26018, Sardinian, P. I. 28954, and P. I. 34272.

A list of the hybrids selected with the parentage and the years the crosses were made is given in the appendix.

Apricot Breeding in Other Countries

A program of apricot breeding has been under way for some time under the supervision of the Department of Agriculture at the Yanco Experiment Farm, Sydney, New South Wales. The work has for its object the production of superior canning varieties, particularly later varieties than Trevatt, to extend the season and thus close the gap of ripening between the latest canning apricots and the earliest canning peaches. Importations of seed have been made from Palestine, Iraq, Syria, and Morocco, and from this material seedlings are now being grown. The varieties used in the crosses and for open pollination are Alsace, Bouche Peche, Mansfield, Moorpark, Lossie Blenheim, Tilton, Campbellfield, Bathurst, Trevatt, Newcastle, and Rose de Vaucluse. From results obtained to date, Moorpark seems to be the best parent variety for giving a useful range of seedlings, while Trevatt cross-bred seedlings have better general quality. A Moorpark × Bouche Peche seedling is being propagated for orchard trial.

In Morocco, work is being carried on at the new State station at Ain Taoujdat, especially designed for research in horticultural genetics. New varieties of high quality are being sought for by hybridization. Ten distinct forms of native apricot (mechmech) have been studied comparatively since 1934 for their value as stocks. Superiority has been shown by E. F. 136, 137, and 139.

Genetic and Cytological Studies With Apricots

There is little published information dealing with the genetics of hybrid progenies of apricot varieties and species.

Cytological studies have been made at the agricultural experiment stations of New York and California, and all apricot varieties examined thus far have 16 as the diploid ($2n$) number of chromosomes, which is the number found in sweet cherry, peach, and some species of plum. At the New York (State) Agricultural Experiment Station, chromosome numbers in exceptionally vigorous seedlings and also in abnormal seedlings from embryo cultures have been counted, but in a total of about 50 cases no deviation from the regular diploid type was found. Unsuccessful attempts have been made to induce polyploidy by selecting giant pollen grains under the microscope, mounting them on hairs, and applying them to the stigmas of flowers. Radiation experiments with stem meristem have also failed. This work is being continued, and other methods to induce polyploidy in apricots are being tried.

Cytological investigations are under way at the California station to determine the true hybridity of the plumcots. This is important in breeding work, to determine whether the characters in segregation will behave as true hybrids or whether they will behave separately as plums or apricots.

Appendix (Apricot)

Table 9.—*Locations of apricot-breeding work and names of workers in the United States and other countries*

State or country, and institution	Location	Workers actively engaged
California:		
Agricultural Experiment Station	Davis	W. P. Tufts, E. C. Hughes.
U. S. Department of Agriculture	do	J. R. King.
Do	Palo Alto	W. F. Wight.
New York: Agricultural Experiment Station.	Geneva	R. Wellington, Olav Einset.
North Dakota:		
Agricultural Experiment Station	Fargo	A. F. Yeager.
U. S. Department of Agriculture	Mandan	W. P. Baird.
South Dakota: Agricultural Experiment Station.	Brookings	N. E. Hansen.
Utah: Agricultural Experiment Station	Logan	F. M. Coe.
New South Wales: Department of Agriculture.	Sydney	H. Wenholz.
Morocco: Experimental Laboratory	Ain Taoujdat	Ch. Miedzyrzechi.

Table 10.—*Apricot seedlings growing at the California Agricultural Experiment Station, Davis, Calif.* [1]

Year of cross	Seedlings planted	Parents	Year of cross	Seedlings planted	Parents
	Number			*Number*	
1931	72	Tilton × Moorpark.		57	Royal × Grace.
	574	Royal × Newcastle.	1932	8	St. Ambroise × Tilton.
	104	Royal × Hemskirke.		22	St. Ambroise × Moorpark.
	226	Royal × Moorpark.		8	Peach × P. I. 38281.
	230	Royal × Tilton.		4	Peach × Tilton.
	31	Wenatchee Moorpark × Tilton.		43	Wenatchee Moorpark × Oullins Early.
	2	Wenatchee Moorpark × Royal.			
	21	Hemskirke × Tilton.		1	Derby × Alameda Hemskirke.
	5	Hemskirke × Moorpark.	1933	2	Newcastle × Peach.
	149	Hersey Moorpark × Royal.		1	Tree (22-1) × Peach.
	33	Blenheim × self.		1	Royal × *Prunus pseudocerasus*.
	7	St. Ambroise × Royal.		1	*Prunus mume* × Royal.
	93	St. Ambroise × Tilton.	1934	1	Pringle Late × Rutland plumcot.
	172	St. Ambroise × Moorpark.			
1932	13	Royal × Peach.		1	Diamond Jubilee nectarine × Royal.
	10	Royal × Wenatchee Moorpark.			
	185	Royal × Oullins Early.		1	Lovell peach × Royal.
	25	Royal × Alameda Hemskirke.			

[1] Verification of the nomenclature used in this and the following lists has not been possible in all cases. Where doubt exists as to the identity of a variety referred to by a name of uncertain validity, no attempt has been made to bring such name into conformity with the code of nomenclature, as it might later result in confusion.

Apricot-Breeding Material at the California Agricultural Experiment Station, Davis, Calif.

Prunus armeniaca:
- Alameda Hemskirke
- Alexander
- Alexis
- Bairam Ali
- Barry
- Beaugé
- Bizant Royal
- Blackmon
- Blenheim
- Blush
- Bolton
- Boulbon

Prunus armeniaca—Con.
- Brady
- Breda
- Budd
- Burtons Royal Seedling
- B. W. Marshall
- Catharine
- Chinese
- Cluster
- Colorado
- Cream
- Crisomelo
- Cutler

Prunus armeniaca—Con.
- Derby Royal
- Di Breda
- Early Cluster
- Early Golden
- Early May
- Garlach
- Giallo di Tortona
- Gibb
- Gilbert
- Great Plains
- Giffin Choice
- Grosse Pêche

Prunus armeniaca—Con.
Gross Blanca Precoce
Harris
Hemskirke
Hersey Moorpark
Janet
Jones
Kaleden
Knobel Blenheim
Lampasas
Large Early Montgamet
Lewis
Losse Blenheim
Lowe
Luizet
Mammoth White
Maxson
McKinley
Meyer Giant
Miner
Mognaga
Montgamet
Moorpark
Murgab
Nellie
Newcastle
New Large Early
Nicholas
Noble
Oullins Early

Prunus armeniaca—Con.
Particolare
Paviot
Peach
P. I. 20072
P. I. 28960
P. I. 34265
P. I. 34270
P. I. 38281
Pringle
Pringle Late
Red Beauty
Riland
Rivers
Rivers Early
Routier Peach
Royal
Rualt
Santa Fe
Sardinian
Sharpe
Shense (Casaba, Acme, Yakimene)
Sloan
Smyrna
Snowball
Sophia
Sparks Mammoth
St. Ambroise
Stella

Prunus armeniaca—Con.
Stephens
Stewart
Sugar
Superb
Tentazione
Thissell
Thompson Early
Tilton
Toyahvale
Trevatt
Upham No. 1
Upham No. 3
Wenatchee Moorpark
Wiggin
Wilson
Zuccherino di Holub

Prunus armeniaca, var. *ansu* Maxim.:
Apricot Plum

Prunus dasycarpa:
Black
Florizan
Prunus dasycarpa No. 13

Prunus mume:
Bongoume
Double Flowering
Japanese (P. I. 45523)

Prunus brigantiaca Vill.
Prunus sibirica

Apricot Hybrids Produced and Under Test at Palo Alto, Calif., in Cooperation Between the United States Department of Agriculture and Leland Stanford Junior University

Year	*Parents of hybrids*
1923	Bergetti × Montgamet.
1931	(Bergetti × Montgamet 30–37[1]) × (Blenheim × Tilton 27–50).
1934	(Bergetti × Montgamet 30–36) × Bremner.
1932	(Bergetti × Montgamet 30–36) × (Moorpark × Blenheim 28–52).
1923	Blenheim × McKinley.
1935	(Blenheim × McKinley 27–21) × (Blenheim × Moorpark 12–58).
1920	Blenheim × Moorpark.
1932	(Blenheim × Moorpark 12–55) × Japanese seedling 26–19.
1932	(Blenheim × Moorpark 12–59) × (Sparks × Blenheim 37–60).
1935	(Blenheim × Moorpark 12–58) × 75222 Tunis 27–70.
1935	Blenheim × (Sardinian × Royal 37–56).
1923	Blenheim × Tilton.
1934	(Blenheim × Tilton 27–50) × (Bergetti × Montgamet 30–35).
1933	(Blenheim × Tilton 28–6) × (Blenheim × Moorpark 12–59).
1934	(Blenheim × Tilton 27–50) × (Blenheim × Tilton 28–6).
1934	(Blenheim × Tilton 28–7) × (Blenheim × 28954 13–26).
1932	(Blenheim × Tilton 27–47) × Bremner.
1931	(Blenheim × Tilton) × Hemskirke.
1935	(Blenheim × Tilton 28–6) × Japanese seedling 26–18.
1932	(Blenheim × Tilton 27–50) × (Moorpark × Blenheim 28–52).
1932	(Blenheim × Tilton 28–6) × (Sparks × Blenheim 37–60).
1933	(Blenheim × Tilton 28–7) × (Blenheim × Tilton 27–50).
1934	(Blenheim × Tilton 27–50) × (34272T2 × Blenheim 12–51).
1921	Blenheim × 28954.
1934	Bremner 9–27 × (Blenheim × 28954 13–26).
1933	Cirio 13–5A × (Blenheim × Moorpark 12–59).

[1] Numbers following variety name refer to row and tree location of the parent.

Year	Parents of hybrids
1924	"Crow apricot seedling".
1920	*Prunus dasycarpa* × Blenheim.
1927	Giallo di Tortona × Moorpark.
1932	Giallo di Fortona × (Moorpark 9–16 × Japanese).
1933	Hemskirke × (Blenheim × Tilton 27–50).
1935	Japanese seedling [2] 26–18 open 27–34C × (Blenheim × Moorpark 12–58).
1935	Japanese seedling 26–18 × (Sardinian × Royal 37–56).
1923	Luizet × Moorpark.
1931	(Luizet × Moorpark 28–39) × Blenheim.
1923	Moorpark × Blenheim.
1931	(Moorpark × Blenheim 28–52) × (Blenheim × Moorpark 12–56).
1932	(Moorpark × Blenheim 28–42) × (Blenheim × Tilton 28–6).
1935	(Moorpark × Blenheim 28–52) × (Sardinian × Royal 2–25 37–56).
1923	Moorpark × Tilton.
1931	(Moorpark × Tilton 28–13) × Hemskirke.
1933	(Moorpark × Tilton 28–12) × (Moorpark × Blenheim 28–52).
1921	Moorpark × P. I. 28954.
1932	(Moorpark 15–28 × P. I. 28954) × Bremner.
1932	Newcastle II 27–16 × Japanese seedling.
1923	Royal × Blenheim.
1933	Royal × (Blenheim × Tilton 28–6).
1935	Royal × Japanese seedling 26–18.
1923	St. Ambroise × Luizet.
1931	Sardinian × Japanese seedling.
1925	Sardinian × Royal.
1925	Sparks Mammoth × Blenheim.
1935	(Sparks Mammoth × Blenheim 37–59) × (Blenheim × Moorpark 12–58).
1932	(Sparks Mammoth × Blenheim 37–59) × Bremner.
1923	Tilton × Moorpark.
1933	(Tilton × Moorpark 30–23) × (Blenheim × Tilton 27–48).
1933	Tunis 27–7A × (Moorpark × Blenheim 28–52).
1920	P. I. 34272T2 × Blenheim.
1932	(P. I. 34272 × Blenheim 12–50) × (Sparks Mammoth × Blenheim 37–60).

Apricot Breeding Material at the New York (State) Agricultural Experiment Station, Geneva, N. Y.

Criscmelo seedling, P. I. 34269.
Geneva.
Henderson.
Ispharak Kandak (Russia).
Murgab (P. I. 32834).
Mulla-gadai (Russia).
Paviot (Germany).
Rittenhouse.
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Ungarishe.

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IMPROVEMENT OF SUBTROPICAL FRUIT CROPS: CITRUS

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MORE than half of the 13 fruit crops known to have been cultivated longer than 4,000 years, according to the researches of De Candolle (*7*)[1], are tropical and subtropical fruits—mango, olive, fig, date, banana, jujube, and pomegranate. The citrus fruits as a group, the lychee, and the persimmon have been cultivated for thousands of years in the Orient; the avocado and papaya were important food crops in the American Tropics and subtropics long before the discovery of the New World. Other types, such as the pineapple, granadilla, cherimoya, jaboticaba, etc., are of more recent introduction, and some of these have not received the attention of the plant breeder to any appreciable extent.

Through the centuries preceding recorded history and up to recent times, progress in the improvement of most subtropical fruits was accomplished by the trial-error method, which is crude and usually expensive if measured by modern standards. With the general acceptance of the Mendelian principles of heredity—unit characters, dominance, and segregation—early in the twentieth century a starting point was provided for the development of a truly modern science of genetics.

In this article it is the purpose to consider how subtropical citrus fruit crops have been improved, are now being improved, or are likely to be improved by scientific breeding. Each of the more important crops will be considered more or less in detail. Before proceeding to these considerations, however, it is desirable to define the province of subtropical fruit culture and to take a glance at the economic importance of the subtropical fruit industry.

The region where subtropical fruits are produced, as the name indicates, is between the true Tropics, where frost never occurs, and the temperate region, where normally the temperature often falls below freezing and stays below for a considerable part of the winter season. In this intermediate region the temperature occasionally goes below freezing but not as a rule below 25° F., so that when necessary the trees can be economically protected by artificial means. Because of the influence of large bodies of water, the protection of mountain ranges, or planting where the topography gives good air drainage, this type of region may be extended as "islands" considerably beyond the usual subtropical region.

The types of fruit crops grown merge into those of the true Tropics—citrus, avocado, mango, etc.—and no hard and fast division can be

[1] Italic numbers in parentheses refer to Literature Cited, p. 806.

drawn on the basis of fruit types except that forms possessing resistance to low temperature are of major importance in the subtropics. Diverse types are cultivated, of which the familiar citrus fruits are among the most outstanding, followed by the pineapple, fig, olive, avocado, date, persimmon, mango, papaya, guava, pomegranate, lychee, granadilla, cherimoya, loquat, jujube, and other minor types.

In the United States some of the crops, notably citrus and avocado, have become staple dessert and salad fruits. Others, notably the date and the fig, are used primarily as confections. The olive is used in preserved form or for oil. Some of these fruits were recognized as important sources of indispensable vitamins even before the true function of these chemical regulators was fully understood. Limes, for instance, have long been included by the British as a regular part of the diet of seamen as a preventive of scurvy. During the recent Ethiopian campaign, the entire Italian export crop of lemons was reserved for the army of invasion, and it is reported that deficiency diseases were at a minimum. Besides the citrus group, pineapples, papayas, dates, avocados, mangoes, and other subtropical fruits are known to be unusually high in vitamins.

Some of these fruits, for example the mango and the papaya, are extensively cultivated but primarily for local consumption. Higgins and Holt (*30, p. 17*) remark: "Excepting the banana, there is no fruit grown in the Hawaiian Islands that means more to the people of this Territory than the papaya, if measured in terms of the comfort and enjoyment furnished the people." This applies to the papaya in other tropical countries as well; to the avocado in Central America and the West Indies; and to the mango in India, southeastern Asia, Malaya, Puerto Rico, and the West Indies in general.

OUTSTANDING *in the story of citrus fruit improvement was the work of A. D. Shamel, of the United States Department of Agriculture, and his coworkers, in studying bud mutations. In the past 18 years, probably 10 million buds of superior strains of the Washington Navel orange, the Valencia orange, the Marsh grapefruit, the Eureka lemon, the Lisbon lemon, and miscellaneous citrus varieties have been sold to California growers alone as a result of this work. Two special strains produced fairly recently—the Robertson Navel orange and the Dawn grapefruit—are now being widely distributed and seem to have great promise. In addition, the intensive study of bud mutations, backed by careful statistics, was important in teaching growers to keep a close watch for branches mutating toward poor types, so that they could be eliminated from the orchard.*

The subtropical fruit production regions in the continental United States are indicated in figure 1. The annual farm value (1934–35) of the chief subtropical fruit crops grown in the United States for

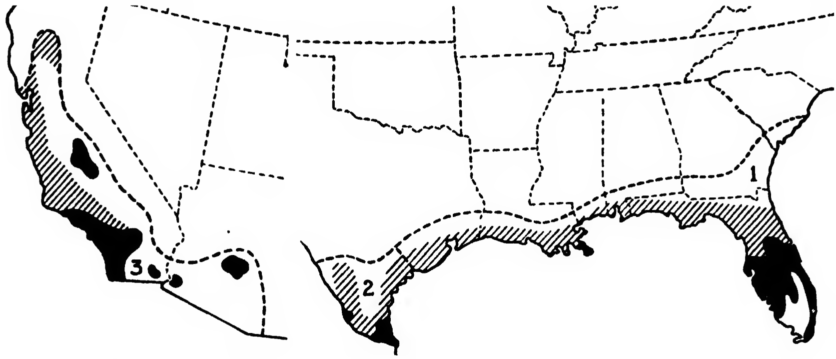

Figure 1.—Citrus-producing areas of the United States. Solid black denotes areas of commercial production of sweet and tangerine oranges, grapefruit, or acid citrus fruits (lemons or limes). Shading denotes areas producing satsuma oranges or minor quantities of other citrus fruits. The dotted boundary lines indicate the approximate northern limits of the three subtropical crop regions: (1) Southeastern humid, (2) central irrigated, and (3) southwestern irrigated.

which figures are available—citrus, fig, olive, avocado, and date—amounts to approximately $140,000,000, distributed as follows: Citrus fruits, $135,000,000; fig, $1,706,000; olive, $1,260,000; avocado, $959,000; date, $390,000.

The distribution of the total return for citrus fruits in the United States in 1934 is given in table 1.

TABLE 1.—*Citrus production in the United States 1934*

[From the United States Department of Agriculture, Agricultural Statistics, 1936]

Fruit	State	Total production	Price per box	Total value
		Boxes	*Dollars*	*Dollars*
Oranges	California	41, 565, 000	1. 80	74, 817, 000
	Florida	15, 500, 000	1. 55	24, 025, 000
	Texas	595, 000	1. 05	624, 750
	Arizona	170, 000	1. 50	255, 000
	Alabama	140, 000	1. 15	161, 000
	Louisiana	293, 000	1. 25	366, 250
	Mississippi	88, 000	1. 30	114, 400
Total or average		58, 351, 000	1. 72	100, 363, 400
Grapefruit	Florida	12, 500, 000	. 91	11, 375, 000
	California	1, 788, 000	1. 10	1, 966, 800
	Texas	2, 720, 000	. 85	2, 312, 000
	Arizona	1, 240, 000	. 85	1, 054, 000
Total or average		18, 248, 000	. 92	16, 707, 800
Lemons	California	7, 500, 000	2. 30	17, 250, 000
Limes	Florida	8, 000	3. 50	28, 000
Total				134, 349, 200

EARLY HISTORY OF CITRUS FRUITS

THE citrus fruits as a class are native to southeastern Asia—eastern India, Indo-China, southern China, the Philippines—and here they were first brought under cultivation. A monograph on the oranges of Wenchow, Chekiang, Nan Yen-Chih's Chu Lu, composed in China during the period 1174 to 1189, is the earliest treatise on citrus culture extant (*26*). Even at this early date three horticultural groups of oranges were recognized and the total number of varieties listed was 27.

Although there are a dozen or more types of citrus fruits, only five or six are of major importance from a commercial standpoint. The most important of these grown for fruits are the sweet orange, *Citrus sinensis* (L.) Osbeck; the grapefruit, *C. grandis* (L.) Osbeck[2]; the acid citrus fruits, including the lemon, *C. limonia* Osbeck, and the lime, *C. aurantifolia* (Christm.) Swingle; and the mandarin orange group, including the tangerine orange, *C. nobilis* var. *deliciosa* Swingle, and the satsuma orange, *C. nobilis* var. *unshiu* Swingle. Other types that are of importance mainly as rootstocks are the sour or Seville orange, *C. aurantium* L.; the rough lemon, *C. limonia* Osbeck; and the trifoliate orange, *Poncirus trifoliata* (L.) Raf. In some foreign countries the sour orange, the pummelo (*C. grandis*),[2] and the citron (*C. medica* L.) are of relatively greater commercial importance than in the United States.

From the Orient the various types and varieties spread to other parts of the world along the trade routes. The citron reached the Mediterranean region at an early date, as it is mentioned by Theophrastus. The sweet orange was apparently not introduced into Europe until the early fifteenth century. The sour orange reached Spain by way of northern Africa. The lemon and the lime were apparently introduced into Europe about the same time as the sweet orange, and several varieties are described by Ferrarius and other writers. Lemon culture first became important in Sicily, Corsica, Genoa, and other parts of southern Europe.

On his second voyage to the New World in 1493 Columbus stopped off for 2 days early in October at Gomera, Grand Canary Island, where he purchased livestock and fruit and vegetable seeds, among which were "seeds of oranges, lemons, and citrons." He reached the island of Hispaniola on November 22, 1493, and in the course of establishing a colony he "set out orchards, planted gardens" (*40*). The historical records of introduction to other parts of the Americas have not been exhaustively searched, but citrus fruits were established at St. Augustine, eastern Florida, by 1579 (*12*) and in Peru before 1591 (*82*). They were introduced into southern California in 1769 by Franciscan monks at San Diego (*43*), and there were undoubtedly many similar introductions into Brazil, Mexico, and other regions settled by the Spanish. In Florida the sour orange, and to a lesser extent the sweet orange and the lime, escaped to the wild.

It is now known, however, that the so-called "wild lime groves" on the lower east coast keys of Florida were in fact planted out by

[2] *Citrus grandis* (L.) Osbeck, as here used, includes the type, the sour shaddock; and two varieties, (1) the commonly known grapefruit and (2) the pummelo, used solely as a salad fruit as explained in the text. The term pummelo should not be confused with pomelo, sometimes used as a synonym for grapefruit.

Henry Perrine, to whom in 1838 Congress had granted a tract of land 6 miles square on Biscayne Bay for the establishment of economic tropical plants. Before his death in the Indian Key massacre of 1840 he had established a nursery of upward of 200 species and selected varieties of useful tropical plants (*53*).

REGIONAL CHARACTERISTICS IN THE UNITED STATES

Commercial citrus growing in the United States presents striking contrasts, due primarily to climatic conditions in the main centers of production (fig. 1). In Florida at an early date the sweet orange, the tangerine orange, and the grapefruit found a congenial home; in California the sweet orange and the lemon have proved the basis for profitable industries, with grapefruit secondary in importance. Texas and Arizona have more recently come into the picture, especially for grapefruit production.

Differences in varieties and seasons of maturity are likewise in sharp contrast. In California two varieties of oranges, the Washington Navel and the Valencia, furnish fruit maturing from November to November, a year-round shipping season. In Florida three or four sweet orange varieties, together with seedlings, are generally required to give a shipping season from October to May. In California lemons are more or less everbearing, affording a supply throughout the year. The Florida and Texas grapefruit crops mature practically during the same season (the fall and winter months), the California and Arizona crops coming in somewhat later. Similar contrasts are to be noted with the rootstocks used in these regions. These and other regional contrasts will be discussed more in detail later.

Thus it will be seen that because of differences in climate and in variety adaptation, citrus fruits, with their highly important vitamins, are available to the American consumer throughout the entire year. In general it may be said that grapefruit has been America's chief contribution to citrus culture, its recognition in Florida as an appetizing breakfast fruit gradually changing this curiosity of the citrus family into a formidable rival of the sweet orange in the national dietary.

Southeastern Humid Region

In the southeastern humid subtropical crops region, citrus development began in eastern Florida in the vicinity of St. Augustine and along the Indian River and in north-central Florida in the general vicinity of Palatka and Ocala as far south as Lake Monroe. On the west coast of Florida the development took place in the vicinity of Tampa Bay and southward. The outstanding pioneers in the introduction of citrus varieties during this period (1870–95) were E. H. Hart (fig. 2); H. S. Sanford, and Lyman Phelps. By the 1880's the industry in northeastern Florida was fairly important, but in the winter of 1894–95 it was practically wiped out by two severe freezes, and the center of the industry was moved farther south to the central ridge section and the southern coastal areas, where most of the citrus growing is now located. Today the industry is based primarily on the sweet orange, grapefruit, tangerine, and lime.

On the upper Gulf coast a citrus industry was established in the Delta district south of New Orleans, based primarily on the sweet

orange. Satsuma growing along the St. Johns River and near Jacksonville began about 1900, spreading thence westward—because of the cold resistance shown by this type during the 1894–95 and 1899 freezes—to the Gulf coast region in western Florida, Alabama, Mississippi, Louisiana, and Texas.

The early plantings of sweet oranges made in various parts of Florida consisted primarily of groves established from seedlings, and it was only later that the practice of budding improved varieties was gradually adopted with the introduction of meritorious early, midseason, and late sorts, beginning in the late 1870's. Since the citrus tree is relatively long-lived, the seedling groves, producing fruit mostly midseason in maturity, are still an important factor in Florida, and they produce approximately 30 to 40 percent of the State's total midseason sweet orange crop. However, budded varieties of recognized merit have been used almost entirely in new plantings and replacements for the last 40 years.

Figure 2.—Edmund H. Hart (1839 98), recognized as a skilled horticulturist and a pioneer in Florida citrus culture. His name is chiefly associated with the Hart's Late or Tardiff orange, now called Valencia, which he first brought to fruiting and introduced into general use in Florida during the 1870's.

Grapefruit first attained commercial importance in the United States. This was between 1880 and 1885, when the first grapefruit were shipped from Florida to the Philadelphia and New York markets. In Florida the industry received a set-back on account of the freeze of 1894–95, but it gradually expanded again, reaching a peak by 1929.

The lemon and the lime, which were classed together in early times, were introduced into the New World by the early Spanish explorers and settlers. The everbearing and rough lemons were among the early introductions into Florida, and the latter had escaped to the wild by the time permanent settlements became common.

Prior to the great freeze of 1894–95 the lemon industry of Florida was of considerable commercial importance. During the year previous to the freeze the annual shipments amounted to 140,000 boxes of lemons. Up to the present the industry has not been rebuilt, but recently attempts have been made to reestablish it. Limes are grown in southern Florida, chiefly on the keys, in Dade county, and in the south-central ridge section.

The mandarin oranges include the King, tangerine, and satsuma types. The tangerine was introduced into Europe from the Orient during the first half of the nineteenth century and was produced on

a commercial scale in Italy as early as the 1840's. It was introduced into Louisiana between 1840 and 1850 and later was brought to Florida, where it is grown as a fancy fruit to a greater extent than in California or Texas. Another member of this group, the satsuma, is outstanding in being the most frost-hardy of all the larger fruited citrus types. It is grown primarily in the upper Gulf coast region, with the chief center of production in western Florida and southern Alabama and Mississippi

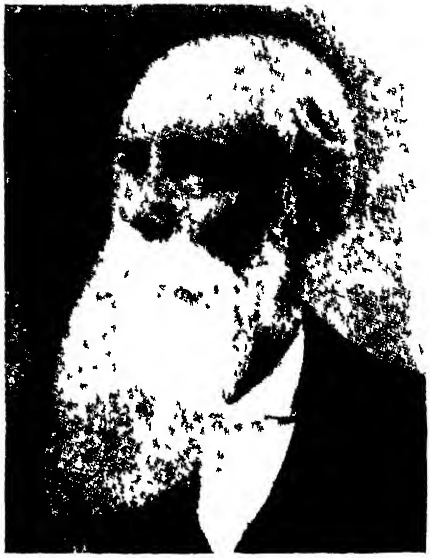

Figure 3.—Thomas A Garey (1830–1909), pioneer California nurseryman, who made extensive introductions of citrus varieties during the period 1868–75.

Southwestern Irrigated Region

In the southwestern irrigated subtropical crops region a citrus industry has been established in California, primarily in the southern coast and interior valley sections. In the southern coast section the industry is based almost entirely on sweet orange and lemon, and in the interior valley section on sweet orange and grapefruit. An extension into the irrigated section of Arizona occurred later, founded primarily on the grapefruit.

Citrus seeds were disseminated from other parts of Mexico to the peninsula of Baja (Lower) California probably in the early 1700's, and later, in 1769, were introduced to Alta (Upper) California by Franciscan missionaries, who established a chain of missions for 400 miles along the coast. According to Coit (*11*), the early settlers secured orange trees from the missions, and a number of small plantings were found in private gardens in the 1830's and 1840's in the vicinity of Los Angeles. These early plantings stimulated further interest, and in 1857, trees were planted at old San Bernardino and Highlands, in 1865 at Crofton, and in 1871 on land now occupied by the city of Riverside. T. A. Garey (fig. 3), of Los Angeles, the outstanding nurseryman of that time, imported large numbers of important varieties during the period 1868 to 1875. His introductions were apparently from Florida, Australia, and southern Europe, as well as from Ellwanger & Barry, of Rochester, N. Y., and Sir Thomas Rivers, of Sawbridgeworth, England. In the southern and central parts of California the industry was only of local importance until after the completion of the Southern Pacific Railroad in 1876, when the first carload of fruit was shipped to St. Louis, Mo., arriving in good condition after a month in transit.

The grapefruit industry in the Southwest—California and Arizona—began after the introduction of the Marsh variety in 1890; the plantings of other varieties previous to that time did not prove profitable.

Great success in lemon culture has been achieved in California, particularly in the southern coastal region, which produces a large proportion of high-priced summer fruit.

Central Irrigated Region

In the lower Rio Grande Valley of Texas, in the central irrigated subtropical crops region, an industry has been established based primarily on the grapefruit and to a lesser extent on the sweet orange.

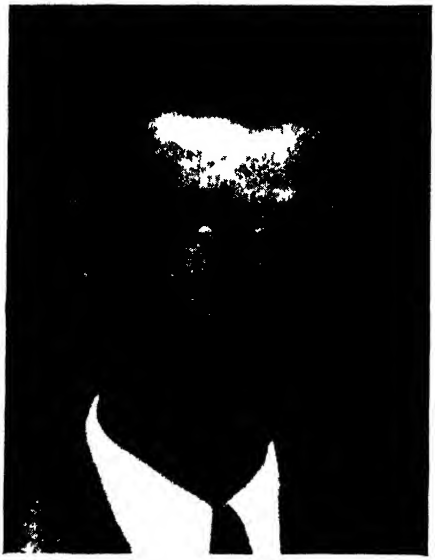

Figure 4.—Charles J. Volz, pioneer Texas citrus grower since 1908, who demonstrated the value of sour-orange rootstock for citrus in the lower Rio Grande Valley of Texas. This demonstration proved to be a turning point in the development of the citrus industry in that section.

As early as the middle of the last century scattered plantings of a few citrus trees could be found along the Texas Gulf coast, particularly from Victoria County southward to Brownsville on the Rio Grande. Experience had demonstrated by the beginning of the twentieth century that regular citrus crops could not be expected in the region above the lower Rio Grande Valley, on account of damage from low temperature (*48*). In the lower Rio Grande Valley—Cameron, Hidalgo, and Willacy Counties—the development of the industry may be grouped into three periods. (1) Up to 1899 citrus fruits were grown for home use and no particular attention was given to the subject of rootstocks. Seedlings and budded trees were planted. During this period, in 1869, the trifoliate orange was imported from northern China by William Saunders, of the United States Department of Agriculture, and it was used to some extent as a rootstock. (2) The resistance to frost shown by trees budded on trifoliate stock during the severe freeze of 1899 led to the extensive use of this stock during the following decade (*87*). Although the stock was valuable from the standpoint of frost resistance and encouraged the pioneer growers to make further attempts, it had the serious defects of dwarfing the scion variety and of being itself subject to foot rot and cotton root rot (*77*). (3) The observations of some of the outstanding pioneers, Charles J. Volz, Harry Banker, J. R. Robertson, F. E. Elliot, Max Melck, and A. P. Wright, beginning after 1900, made possible the growing of citrus fruits in commercial quantities.

Charles J. Volz (fig. 4), from Indiana, settled near Mission in Hidalgo County, Tex., in 1905. He began the planting of citrus in 1908 and clearly demonstrated the superiority of the sour-orange rootstock under the lower Rio Grande Valley conditions. Harry

Banker, from Oklahoma, who settled near Brownsville, in Cameron County, secured similar results with the sour-orange rootstock beginning in 1910 (*87*). With the solution of the rootstock problem the industry showed at first gradual and later rapid development. The citrus shipments from this section, consisting mainly of grapefruit, had reached 13 carlots in 1921 and increased to more than 5,000 carlots annually by 1931. Yields were cut down as a result of hurricane damage in 1933 and damage due to low temperature in 1933–34 and 1934–35, but the crop of 1936–37 reached a total of over 15,000 carlots. Fortunately for this new industry, the seedless type of grapefruit (Marsh variety and its pink-fleshed mutations) has been most heavily planted in Texas, and this has doubtless contributed to its favorable reception in many markets.

HAWAII, PUERTO RICO, AND THE PHILIPPINES

The sweet orange was introduced into Hawaii in 1792, and many citrus varieties have been cultivated there for over 100 years (*54*). The climate is well adapted to citrus culture, but for commercial production the situation is complicated by the presence of the Mediterranean fruit fly, which limits production to local needs.

While citrus fruits, especially the sweet orange, have been grown in a semiwild condition in Puerto Rico for perhaps 3 centuries, commercial planting did not begin until about 1900. The first plantings were largely of Florida orange varieties, but these were soon largely discarded in favor of grapefruit (*29*). The varieties most commonly grown are the Duncan and the Marsh. For budding stocks, rough lemon, sour orange, and seedling grapefruit have all been successfully used, the rough lemon being favored for rapid growth and early production and especially for the lighter grades of soil. Wind damage has caused frequent losses of trees and fruit and has directed attention to the use of such plants as bamboos and casuarinas for windbreaks.

Owing to the fact that the trees bloom intermittently, Puerto Rico is enabled to ship grapefruit over a long season, a summer crop often maturing from a previous fall bloom. Production for several years past has averaged about a million boxes, of which approximately 25 percent is marketed as canned grapefruit. Puerto Rico is credited with having initiated the canning of grapefruit "hearts", a product that has grown rapidly in favor and has made grapefruit available at all seasons and in many localities where fresh fruit seldom is offered. Orange shipments from Puerto Rico, amounting to a half million boxes in good seasons, consist largely of so-called "wild oranges", which come in a considerable measure from seedling trees cultivated as shade trees on coffee plantations.

In the Philippines citrus fruits have been grown for centuries, forms of *Citrus hystrix* DC. (kalpi), *C. mitis* Blanco (calamondin), and *C. grandis* (pummelo) being native to the islands. It is only in recent decades, however, that attention has been given to growing the fruit commercially. Wester (*88*), beginning about 1910, brought together an extensive collection of citrus varieties at Lamao, few of which proved adapted to Philippine conditions. The mandarin oranges as a class have proved best suited to commercial culture,

and a local variety known as Batangas mandarin is being grown on a considerable scale chiefly for the Manila market. The Batangas, the King, and the Szinkom mandarins, several pummelo varieties—including the Siamese—and the Valencia orange constitute most of the recent plantings. Genetic studies and hybridization work have been inaugurated by Torres, and one hybrid variety, Szinbat (Szinkom × Batangas), has been introduced. It is characterized as productive, of good quality, and resistant to wind injury. Further breeding and selection work is in progress, special studies being made of polyembryony—to be discussed later—in scion and stock varieties.

BREEDING MATERIALS

THE citrus breeder is concerned with two kinds of plant materials within the Rutaceae—the citrus group proper, containing the types closely related to the widely known sweet orange, and various species in genera somewhat less closely related. The first or citrus group contains all of the valuable types cultivated for their fruits or used as rootstocks, and the second is of value in some instances as stocks, as breeding material, and in furnishing a clue to the evolutionary development of the branch of the Rutaceae to which the citrus fruits belong.

The citrus group proper is characterized by great diversity in morphological characters, and this has led some systematic botanists to the multiplication of species. The classification of Swingle (*68*), however, is conservative, has been widely accepted, and is used in this report. The only exception made is in the case of *Citrus grandis*, where it has been necessary to recognize two varieties besides the type species.[3] The horticultural differences in a number of cases are so great, as will be pointed out in the discussion of dessert quality later, that the single type designation is quite inadequate.

The following types commonly grown for their fruits or as rootstocks are in the three genera *Citrus*, *Fortunella*, and *Poncirus*:

Sweet orange, *Citrus sinensis* (L.) Osbeck.
Sour orange, *C. aurantium* L.
King orange, *C. nobilis* Lour.
Tangerine orange, *C. nobilis* var. *deliciosa* (Tenore) Swingle.
Satsuma orange, *C. nobilis* var. *unshiu* (Mak.) Swingle.
Shaddock, *C. grandis* (L.) Osbeck.
Grapefruit, *C. grandis*.
Pummelo, *C. grandis*.
Citron, *C. medica* L.
Lemon, *C. limonia* Osbeck.
Lime, *C. aurantifolia* (Christm.) Swingle.
C. ichangensis Swingle.
Kalpi, *C. hystrix* DC.
Calamondin, *C. mitis* Blanco.
Kumquat, *Fortunella* spp.
Trifoliate orange, *Poncirus trifoliata* (L.) Raf.

The citrus breeder is fortunate in possessing material that presents so many diversities—in dessert and keeping quality, season of maturity, resistance to disease, and regional adaptation. All of these will be developed in detail in the following text, but the dessert quality of the types will be discussed at this point.

[3] See footnote 2, p. 752.

Character and Uses of the Fruits

Some of the fruits listed above—sweet orange, grapefruit, lemon, and lime—have become well known to northern readers and need to be only briefly differentiated; a few, however, are little known and will require more detailed descriptions. In general it may be stated that the taste qualities of mature citrus pulp and juice are dependent on various combinations of sugars, acids, glucosides, esters, and peel oil. The first two, the sugars and acids, are the basic matrix and give variations from sour through tart, sweet, and insipid, and the latter contribute bitter and aromatic principles. The bitter principle, furnished by glucosides, is apparent only if it is in solution in sufficient amount in the juice (*5, 78, 79*). This is normally not the case except in such types as grapefruit and lime. The aromatic quality contributed by peel oil is important in some cases.

In most commercial varieties of sweet orange the sensation of sweetness predominates, combined with a slightly perceptible tartness. In most varieties the quality contributed by esters is slight, but in such varieties as Pineapple the suggestive "pineapple" ester is outstanding.

In the mandarin orange or free-peeling group, the tangerine oranges are characterized by the pleasant "tang", which is due to esters. The King and satsuma oranges in this same group have taste qualities similar to those of the sweet orange.

In grapefruit the bitterness of the glucoside naringin gives the sprightly taste added to the mild acidity that makes the fruit outstanding as a breakfast appetizer.

The pummelo, as distinguished from the sour shaddock, is used only as a salad fruit. The large juice sacs are separated from the locular wall tissues and are served like any other salad. The flavor in the better varieties is due to a very slight acidity and the presence of only a very little glucoside, but it is predominantly sweet, and inimitable quality is contributed by esters.

In lemon and lime, acidity is of first importance. A good acid citrus fruit, as pointed out by Traub and Robinson (*80*), should have from 6 to 7 percent of acid. In lime the characteristic glucoside, which has not been studied in detail, lends the "lime" taste. The peel oil of lemon and lime also gives desirable qualities.

The citron is used entirely as a preserve. The kumquat is used both in preserving and in table decorations. It is also eaten entire, out of hand. Two general types are recognized, sweet and sour, in both of which the rind has little of the pungent oil common to most citrus fruits.

In the case of hybrids, intermediates have in some instances been secured, especially in the tangelo oranges—hybrids between the grapefruit and the tangerine orange. In these hybrids, as a rule, the esters are predominant in distinguishing the flavor of the new fruits from the common sweet orange. In the Perrine lemon, a hybrid between the lemon and the lime, there is a mild suggestion of the lime glucoside.

When hybrids between citrus species first appeared it was customary to apply various compound names, such as tangelo, tangor, oranguma, limelo, lemelo, etc., to indicate the parentage. It was soon realized that this would lead to confusion from the horticultural

viewpoint, since some crosses gave rise to more than one horticultural or market type. The grapefruit-tangerine cross (tangelo), for instance, gave rise to forms like the now generally known tangelo orange, and also varieties that resemble the grapefruit in structure and juice quality but with the rind, flesh, and seed color of the tangerine. A strict application of the term "tangelo" would have included both of these forms. The difficulty was overcome by the decision to place hybrids for purposes of horticultural classification with the well-known types that they most resemble, and to use the interspecies compound designations only in their scientific application. On this basis most of the tangelos already introduced, being more like the sweet orange in structure and use, were designated as a group of the sweet orange, possessing relatively high quality with special reference to a pleasing blending of esters, sugars, and acids. Such a class would naturally contain also such hybrids as the Umatilla (oranguma), a cross between the sweet orange and satsuma orange, but very similar to the other tangelo oranges, and also the Temple, apparently a naturally occurring hybrid between the tangerine and a grapefruit variety similar to the Tresca.

Representatives from a great number of related genera, *Glycomis*, *Claucena*, *Chalcas*, *Feronia*, *Feroniella*, *Aeglopsis*, *Aegle*, *Swinglea* (*Chaetospermum*), *Balsamocitrus*, *Lavanga*, *Hesperethusa*, *Triphasia*, *Severinia*, *Citropsis*, *Atlantia*, *Eremocitrus*, and *Microcitrus*, have been introduced by the United States Department of Agriculture during the last 25 years. These are listed in table 6 in the appendix. Some of these may prove of value in citrus breeding and as rootstocks. Although certain species have entered to some extent into hybridization work, no hybrids of immediate value have been secured up to the present. The material, however, is valuable to the breeder from another standpoint, for it presents an opportunity for an evolutionary approach to the study of relationships within the group.

GENERAL TRENDS AND PROBLEMS

The early history of citrus improvement in the United States is concerned almost entirely with the introduction of varieties from other citrus-producing regions, mainly through private initiative. This period extended to the 1870's in this country. Toward the end of the nineteenth century, in the United States, the number of varieties was increased by the addition of those originating as chance seedlings and possibly by bud mutations accidently propagated. Still later, improved types appeared as the result of artificial cross-pollination. Breeding work was undertaken by the Department of Agriculture in 1892, and the the State agricultural experiment stations in California in 1910, in Florida in 1924, in Alabama in 1933, and in Texas in 1934.

Problems Peculiar to Citrus Breeding

The breeding of citrus fruits presents two problems not met with in the case of the usual annual crops such as grains, which can be grown in great numbers on a relatively small area at small expense.

First, as a rule it takes from 6 to 10 years to fruit a seedling citrus tree unless the variety is top-worked on an older tree, in which case the time will be cut in half. The trees are expensive to produce and to

test out in orchard formation on various soil types and under various climatic conditions. It is necessary, therefore, to plan breeding experiments so that only progeny are grown that promise varieties of immediate value or additions to the knowledge of citrus genetics With such a handicap, the work has not progressed at a very rapid rate.

The other difficulty is due to the phenomenon of polyembryony—meaning "several embryos per seed" (fig. 5). In the case of plants reproducing by seeds, each single seed as a rule gives rise to one seedling, which is the result of the union of the male gamete (reproductive cell), contributed by the pollen grain, and the female gamete (egg cell), contained in the ovary of the flower. In each of these gametes the number of chromosomes has been normally reduced by half preparatory to reproduction (the haploid number of chromosomes), and the union of the two results in a complete complement of chromosomes, called the diploid number, which is characteristic of all of the body cells of the individual plant as distinguished from the sex cells. In the case of the citrus seeds, however, a normal embryo produced by the union of the male and female gametes may be present, and in addition one or more—sometimes as high as 15—additional embryos that have arisen from projections into the embryo sac of the surrounding maternal tissue (nucellar tissue). When these projections develop into embryos they have the full chromosome complement (diploid) of the mother plant without the union of two gametes. Citrus types and varieties may vary greatly in the number of nucellar

Figure 5 — Nucellar embryony in citrus, showing four seedlings sprouting from single seeds (McCarty grapefruit): *A*, One vigorous seedling and three relatively less vigorous; *B*, four vigorous seedlings; *C*, similar to *A* after separation. (See also fig. 17, showing cytological details)

embryos produced. Seedlings that develop from nucellar embryos are called apogamic seedlings (literally, "without marriage").

Unless the parents have unlike vegetative characters, it is not possible to distinguish the sexually produced or hybrid embryo from those that arise by nucellar budding, though in the latter, of course, only the characters of the female parent will appear. This means that a great many more seedlings must be grown to the point where they can be distinguished than in the case of crops producing only normal or seminal seedlings. Citrus breeding, therefore, will continue to be even more costly than ordinary tree-fruit breeding unless a method can be worked out to achieve practical control of nucellar embryony.

Thus it is natural to expect relatively slow progress. The results from cross-pollination followed by inbreeding and selection, and from back-crossing on the parent types, will not be available in a few seasons but only after a considerable period of time. However, the earlier pioneers in this field have laid the foundation, and in the future it is probable that the rate of progress can be considerably accelerated.

Methods of Breeding

Fortunately no problem is presented with reference to controlling pollination in citrus. The flowers are relatively large and the ordinary bagging technique with brown-paper bags has proved sufficient. In practice the flowers are emasculated before pollen is shed and then bagged. They are pollinated soon after opening, and the bags, which were removed for pollination, are replaced and left on until the petals have fallen and the fruit begins to grow. To protect from loss by dropping, the fruits are usually covered with cheesecloth bags.

Pollen is gathered from flowers that have been bagged when still closed and is used immediately unless flowering of the parents desired does not overlap, in which case the pollen is stored for later use. Kellerman (*35*) has shown that citrus pollen dried over concentrated sulphuric acid and sealed in glass vacuum tubes at about 0.5 mm pressure can be kept in a viable condition for more than 2 months.

When the seeds are removed from the harvested mature fruits secured as a result of artificial pollination, they are thoroughly washed and are planted at once in flats, for the germination percentage usually decreases if they are allowed to dry in the air. The flats containing the seeds are placed in a coldframe to prevent damage by heavy rains. When seedlings are 6 to 18 months old they are planted in nursery rows, usually 12 by 6 feet apart, and given good culture. As soon as the fruiting stage is reached, usually in 5 years, or sooner if top-worked on old trees, detailed records are taken of tree and fruit characters, and all seedlings that show no immediate promise or appear to be of no value for future breeding are destroyed. These records determine the apparent worth, if any, of the plants as varieties for cultivation, and also serve as a basis for working out genetic principles.

The seedlings are tested for vigor, including disease resistance, bearing capacity, and regional and rootstock adaptation. The fruits are tested for size, shape, juice percentage, season of maturity, number of locules and seeds, rind thickness, percentage of "rag", percentage of sugars and acids, effective acidity (pH) of the juice, and the

flavor of the juice. Out of a great number of seedling individuals only a very few are finally selected for introduction, and these are released only after favorable performance in preliminary fruiting tests in a number of locations.

Objectives of the Breeder

The first consideration in citrus breeding is excellent dessert quality. What constitutes high quality has been previously discussed, and we pass to the consideration of tree and other fruit characters that the breeder has in mind when making his crosses and selections.

The tree (scion variety) should be compact in habit, but a vigorous grower and a prolific bearer. It should be resistant to the common citrus diseases and to low temperatures, and congenial with the rootstock or rootstocks used in the region. The fruit should mature at the proper season or seasons to suit market needs. There are also other characters of importance, such as thornlessness.

The fruit should have excellent dessert quality and contain few or no seeds; the shape and size should be suited to commercial requirements and to ease in packing; shipping or keeping quality, including resistance to storage diseases, should be good; the exterior, including texture and color of rind, should be attractive; and, in particular, the vitamin C content should be up to the standard. With the rapid growth of a new industry in canning "hearts" and juice of both grapefruit and orange, special attention may need to be given to the requirements of this promising industry. For instance, it has already become evident that the pulp of Marsh grapefruit lacks the firmness necessary in a good canning grapefruit. With the growing tendency to utilize citrus fruits in juice form and in mixed drinks, the high color of the juice characteristic of the tangelo group of hybrids is proving a decided advantage.

The tree used as a rootstock should be adapted to the soil and climatic conditions, be free from or resistant to trunk and root diseases, and produce a high percentage of nucellar embryos, and it should not be so vigorous in growth as to make the fruit of the scion coarse, of poor texture, and comparatively low in total solids (sugars and acids) and therefore insipid in taste (*6*, *80*).

As the margin between production costs and sales returns becomes narrowed with increasing supplies of citrus fruits, any adaptation that might lessen the cost of production becomes vitally important. This places emphasis on disease resistance in any breeding program, to reduce both expense for grove sanitation and losses due to infected trees and fruit. In citrus the list of such diseases is quite extensive and varies with citrus types and varieties.

The task of breeding for resistance to injury from insect and other animal pests on plants presents the major difficulty of developing a practical technique.

In Florida the chief citrus diseases are melanose, affecting tender twigs, leaves, and immature fruits, and stem-end rot, affecting mature fruit, both caused by *Diaporthe* (*Phomopsis*) *citri* (Fawc.) Wolf; sour orange scab (*Elsinoë fawcetti* Bitancourt and Jenkins), affecting leaves and fruits; key lime anthracnose (*Gloeosporium limetticolum* Clausen); foot rot (*Phytophthora parasitica* Dastur); and psorosis, cause undetermined.

In the Southwest, brown rot gummosis and foot rot (*Phytophthora citrophthora* (Sm. and Sm.) Leonian and *P. parasitica*); psorosis; and shell bark (*Diaporthe citri*) are of major importance; and in the lower Rio Grande Valley gummosis, scaly bark, and stem-end rot (melanose).

Achievements and Future Possibilities

In spite of the peculiar difficulties encountered in citrus breeding, definite achievements can be recorded, and the outlook for the future is most encouraging. The work in the past has shown that worthwhile results may be secured from appropriate crosses and that important strains and varieties may arise by bud mutation. In addition a beginning has been made in laying a foundation of genetic principles.

The work in citrus hybridization carried on by the Department of Agriculture workers since 1893 has shown that the combinations of grapefruit and tangerine and of lemon and lime give the most promising results. The first have given rise to high-quality fruits known as the tangelo oranges, and the latter to a high-quality lemon, the Perrine. The work of Frost, of the California Agricultural Experiment Station at Riverside, has shown that crosses within the mandarin orange group give worth-while results.

Apogamic seedlings from crosses have also given rise to important varieties in grapefruit and in sweet, sour, and satsuma oranges. Bud selection has given superior strains of known varieties and has served to stabilize standard varieties. Crosses with more distantly related relatives of citrus, *Citrus* × *Poncirus*, citrange × *Fortunella*, citrange × calamondin, etc., have proved interesting from the genetic standpoint and have also given some concrete types of possible value in horticulture—citrange, citrangequat, and citrangedin. Reference to particular hybrids in which definite objectives have been attained are found in the text and in table 6.

Thus the ground work has been laid by the earlier workers. With the wealth of breeding material and the increase of interest in this field, research in citrus breeding may be expected to show greater progress in the years to come.

Some idea of what the future holds in store as a result of citrus breeding can best be gained from the following quotations contained in the report made by H. B. Frost, actively engaged in citrus breeding at the Citrus Experiment Station, Riverside, Calif., in connection with the cooperative survey of plant and animal breeding:

> If we wish to produce a variety or strain that is very similar to a standard variety, such as the Valencia, but superior in some important feature, such as eating quality, generative seedlings from either selfing or narrow crossing are very unpromising, for two reasons: (1) they are usually weak and very unproductive, and (2) they are usually very unlike the parent or parents. The best chance of success, although a very uncertain one, seems to lie in the discovery of superior bud-variation forms. Such forms may be found, of course, either as "limb sports" or as whole trees which have happened to be budded from variant branches. They may also be found as seedlings derived from nucellar embryos that happen to be formed on a variant branch; in this case the seedlings are likely to be indistinguishable from other nucellar seedlings until they produce fruit. On the basis of the time and expense required, the search for bud variations in commercial orchards seems more promising than the growing of seedlings. A good new bud-variation type may in some cases, however, be variable because of

mixture with the parent variety in the same shoots to form a chimera, and the growing of seedlings may then be the best method of getting the new type separated from the parent variety. Variability may in some cases be inherent in the constitution of a new form, however, so that it will never become stable.

X-ray treatment probably can be used, as it has been with other plants, to increase greatly the frequency of new genetic variations. It seems most likely to be useful by producing variations in nucellar seedlings.

For the production of new varieties of superior quality but with flavors very unlike those of the present varieties, the great variability of hybrids offers much promise, since we can use wide crosses, which commonly give vigorous hybrids. Various hybrids of the tangelo and tangor groups, which are hybrids of mandarins with grapefruit and with sweet orange, that have been introduced by the United States Department of Agriculture, offer unique and very pleasant flavors. It is now probable, however, that the best opportunities for securing superlative quality are to be found in crossing within the mandarin species or group of species, and therefore, it is very fortunate that certain crosses between mandarin-group varieties produce vigorous hybrids.

It is advisable to make some further trial of the production of triploid hybrids by pollinating tetraploids by diploids of other species (or of other sections of the mandarin "species"). The only tetraploid form which at present seems to have much promise for such use is the tetraploid Lisbon lemon, which combines good seed production, comparatively low chromosome irregularity, and high proportion of generative progeny.

The evidence on which these suggestions are based has only partly been secured at the Citrus Experiment Station, and that on the results of selfing has very largely been obtained in Dr. H. J. Webber's root stock experiments. The nature of the work has ranged from chromosome counts and systematic records of various tree and fruit characters, to the determination of the agreeableness of fruit flavors. Any extensive gene analysis is clearly impracticable in citrus, yet certain evidence has been obtained which seems to have definite significance for general genetic theory, when interpreted on the basis of gene analysis made on more favorable organisms.

The problems that most concern the citrus breeder have been listed by Frost as the determination of—

(1) The generality of the reduction of vigor with selfing and narrow crossing. (2) The extent to which the proportion of nucellar seedlings can be predicted from counts of total embryos. (3) (*a*) The extent to which triploids are unproductive of fruit, as compared with diploids of the same ancestry. (*b*) The extent to which triploids can be produced by crossing diploids with tetraploids. (*c*) The frequency with which triploids occur from crosses between diploids. (4) The extent to which the prospects of high vigor, productiveness, good flavor, and other horticulturally desirable characters in crossing can be inferred from knowledge of the species or smaller taxonomic group to which a variety belongs, on the basis of trial of other varieties of the same group. (5) The frequency with which new genetic types arise by bud variation, and the extent to which this process can be speeded up by X-ray treatment of seeds, pollen, etc. (6) The best methods of modifying physiological conditions to secure high seed production in crossing, and, if possible, high proportions of generative embryos.

With the present facilities, problems named under 1 to 4 above may be solved partially, and to a much smaller extent those under 5 and 6 in the list.

IMPROVEMENT OF CITRUS VARIETIES

The improvement of citrus varieties will now be briefly discussed on the basis of citrus types—sweet orange, mandarin oranges, grapefruit, acid citrus fruits, and minor citrus fruits. In each case the varieties will be considered by regions. Following this, citrus bud selection and citrus rootstocks will be considered under separate headings.

Sweet Orange Improvement

Florida

In Florida the bulk of the citrus crop is produced between October and June. Good early-maturing and very late-maturing varieties are of most importance from the breeding standpoint. The sweet orange varieties of Florida have been described by Hume (*32*).

EARLY VARIETIES

Early-maturing sweet orange varieties for Florida are relatively scarce, and it is desirable to give this fact due weight in any citrus-breeding project.

The Hamlin is one of the early varieties usually recommended. It was discovered in a grove planted in 1879 near Glenwood, which later came into possession of H. E. Hamlin. Under the best cultural conditions the acidity and sweetness are well blended, giving it excellent flavor; the rind is smooth and glossy; seeds are none too few; the season is October and November and later. Recent reports indicate that it is sensitive to overfeeding and other unfavorable growing conditions, which may lead to fruit splitting, riciness of pulp, and poor juice quality.

The Parson Brown variety was introduced by C. L. Carney, of Lake Weir, about 1878, having originated at Webster in a seedling grove owned by Parson Brown. Acidity and sweetness are fairly well blended if the fruit is picked early; seeds, 10 to 19; season, October and November.

Early sweet oranges usually have poor rind and flesh color when harvested at the beginning of the season. This is a deficiency that might be remedied by breeding methods.

The results thus far look promising. A hybrid, the Orlando tangelo orange (fig. 6), introduced by the Department in 1931 and resulting from a cross of the Bowen grapefruit pollinated by Dancy tangerine, is early in maturity and can be harvested over a long season. The variety is highly resistant to citrus scab. When first harvested in late September or early October the rind color after degreening with ethylene is a beautiful light yellow, but later in the season it takes on a natural deep reddish-orange color. It is medium in size, and the flesh color is deep orange. Its main defect is its seediness. Such a defect can apparently be overcome in future breeding work, as will be pointed out later.

MIDSEASON VARIETIES

A large number of midseason varieties were named and introduced beginning in the 1870's. Among these the outstanding ones are the Homosassa and Pineapple. The Homosassa is a variety of excellent quality, with a sprightly, rich, vinous flavor; seeds, 20 to 24; season, December to February. The Pineapple is the outstanding midseason variety, having a glossy rind of deep orange color, vinous and sprightly in flavor; seeds rather large and numerous. It originated near Citra, Marion County, and received its name from the fine aroma reminiscent of the pineapple. It is today the most important midseason sweet orange in Florida.

The navel type of sweet orange is not suited to the Florida climate. Although a number of varieties have been introduced, they have not proved successful as the Washington Navel has in California.

Two midseason tangelo oranges, of the same parentage as the Orlando variety, introduced by the Department in 1931—Minneola (December–January) and Seminole (February–April)—are outstand-

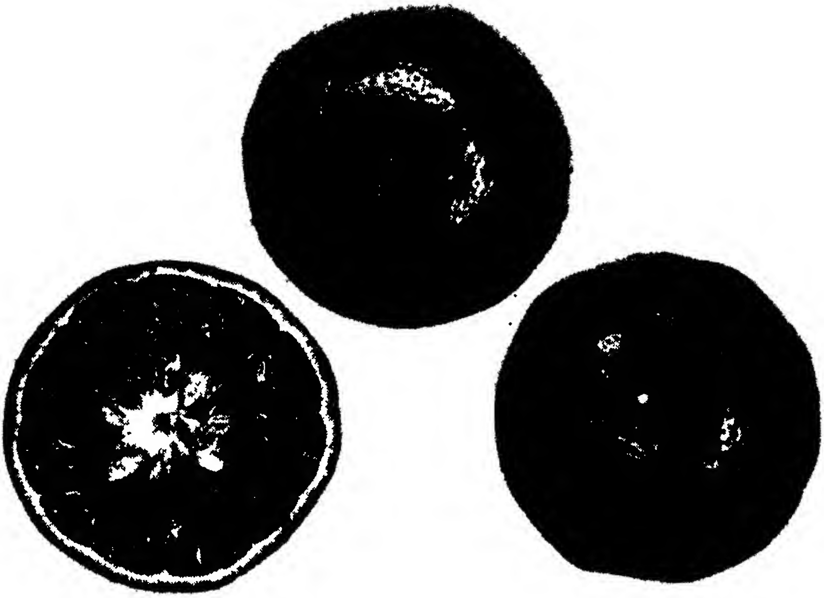

Figure 6.—Typical fruits of Orlando tangelo orange (originally introduced as the Lake variety), a hybrid between grapefruit (♀) and tangerine (♂); remarkable for earliness, maturing in October and November; highly resistant to scab. Introduced by the United States Department of Agriculture.

ing from the standpoint of dessert quality, the Minneola especially having the most delicate blending of esters, sugars, and acids. These fruits have deep tangerine rind and flesh color, and their shipping quality is good. Like the Orlando tangelo orange, the Seminole (fig. 7) is highly resistant to citrus scab, the Minneola partially resistant. The fruits are somewhat seedy.

LATE VARIETIES

The sweet orange industry up to the 1870's was based on seedlings and clones producing early and midseason fruits. An event of great importance took place when, early in the 1870's, the late type of sweet orange, now called Valencia (fig. 8), was introduced into Florida by S. P. Parsons, a nurseryman of Long Island, N. Y., and Palatka, Fla. Parsons had secured it from Thomas Rivers in England, who had imported it from the Azores and had cataloged it under the name "Excelsior." Parsons gave trees to E. H. Hart (fig. 2), of Federal Point,

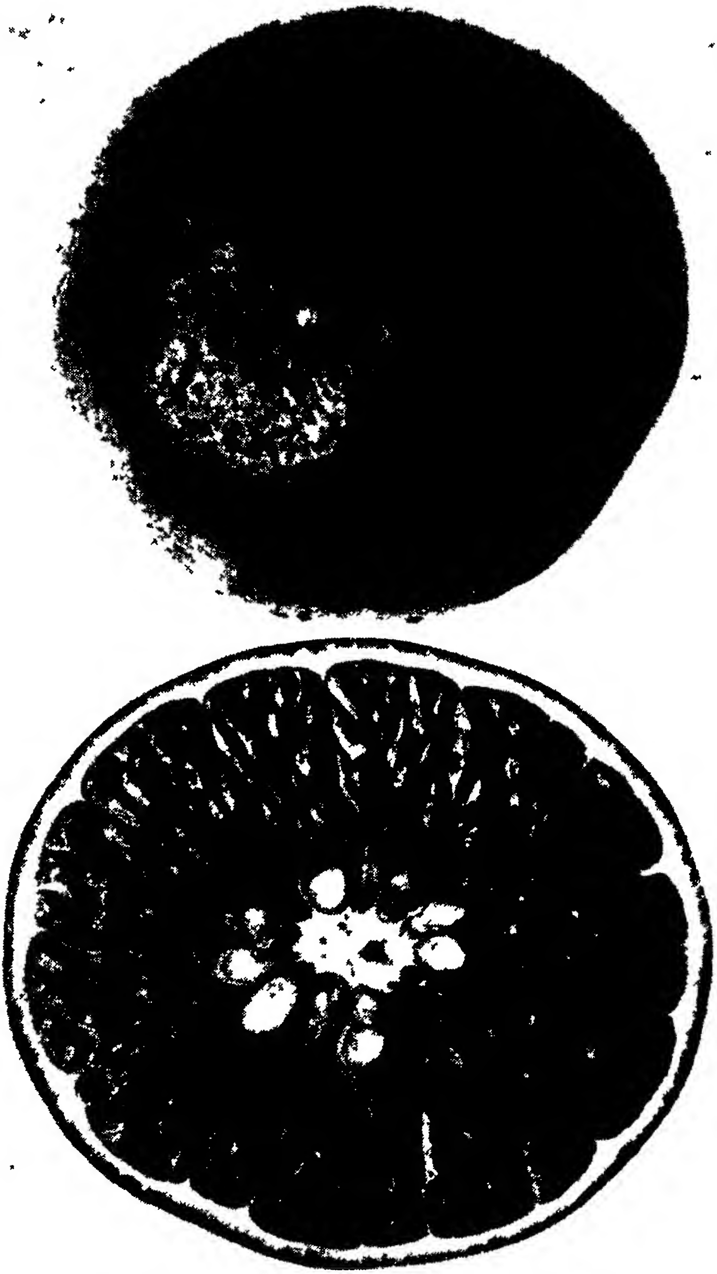

Figure 7.—Typical fruits of Seminole tangelo orange, a hybrid between grapefruit (♀) and tangerine (♂); midseason to late in maturity; replacing the older Sampson variety because of its high color and flavor, resistance to scab, and good shipping quality. Introduced by the United States Department of Agriculture. (Natural size.)

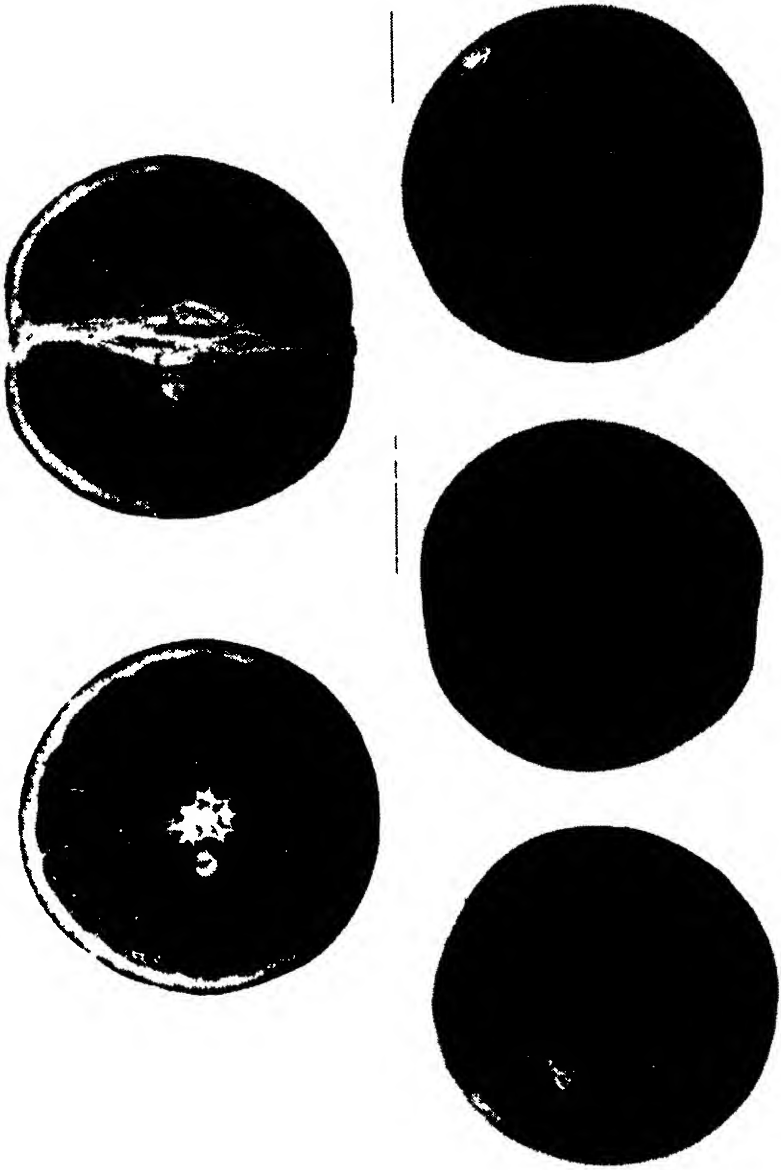

Figure 8.—Valencia orange, typical of the variety as grown on sour orange rootstock in Orange County, Fla. It is characterized by late maturity (March to June in Florida), firm flesh and rind, and fairly high content of citric acid, contributing to its good holding and shipping quality. It is commercially seedless, having normally two to five seeds.

Fla. Having lost the label, Hart distributed the trees under the name of Hart's Late or Hart's Tardiff. The variety was exhibited before the Florida Fruit Growers Association on April 25, 1877. The outstanding characteristic of this variety is its late maturity. Its season extends from March to June.

The variety was also imported into California, in a lot of citrus varieties from Thomas Rivers, by A. Chapman, of San Gabriel, Calif., between 1870 and 1872. One of these varieties, labeled as a navel, turned out to be a late-ripening nonnavel variety that fruited after the other varieties were off the market. The variety was named Valencia at the suggestion of a Spanish laborer, and Chapman sold it under the name of Valencia Late. Nurserymen in California had purchased stocks of Hart's tardiff, and a great many trees had been set out. By the time it was discovered that the Valencia and Hart's Tardiff were identical, the variety had attained commercial importance in California, and the name Valencia was retained.

A variety similar to the Valencia, named Lue Gim Gong, for the originator, and introduced in 1912 by the Glen St. Mary Nurseries, is described as very late in maturity. It is now generally regarded as a strain of Valencia, from which it originated as a seedling.

The production of a tangelo orange (Umatilla), which resulted from the pollination of the satsuma by the Ruby sweet orange and was introduced by the Department in 1931, indicates what may be accomplished by breeding methods in the creation of late-maturing varieties. In contrast with the parents—satsuma, early maturing, and Ruby, sweet midseason—the hybrid matures its fruit in late February, March, and April. The variety is highly resistant to citrus scab; the fruits are medium to large in size; the rind and pulp color is deep orange, and the quality is excellent. Seed content is variable.

To sum up: At the present time the sweet orange industry in Florida is based primarily on two early varieties, Hamlin and Parson Brown; on midseason seedlings and two midseason varieties, Pineapple and Homosassa; and on one late variety, Valencia.

California

In California one early and midseason navel and one late nonnavel variety have proved sufficient to produce an orange crop every month in the year.

Contrary to popular opinion, the navel type of sweet orange is not a modern product. It was described and pictured by John Baptisti Ferrarius in 1646 and is apparently of early origin. As early as 1820 the Bahia form of the navel orange had made its appearance in Brazil, where orange trees had been introduced by the Portuguese settlers. Its excellent qualities were soon recognized, and the variety was extensively propagated in the vicinity of Bahia. Even at this early date the variety seems to have been subject to bud mutation, and inferior types appeared that were unintentionally propagated and introduced in South Africa and Australia. Those that reached Australia also included desirable types.

The Bahia type of navel orange was first introduced into Florida in the 1830's, but the trees were killed during the freeze of 1835. A shy-bearing form of Bahia navel was introduced into California in the

early 1870's. The strain was secured from S. B. Parsons, Flushing, N. Y., who had received it from Thomas Rivers in England. In the early 1870's an inferior type of navel orange was imported from Australia into California, which set the precedent for referring to inferior strains as the Australian navels to distinguish them from the superior Bahia strain.

The story of the Washington Navel orange is a dramatic illustration of the value of superior varieties of economic plants. In 1870 the citrus industry had begun in California, but there was no outstanding early and midseason variety of sweet orange generally adapted to the climate. The early mission seedlings and varieties introduced after the middle of the nineteenth century were being tested out by various growers, but there was a lack of standardization in quality. The value of alertness in using the plant material that has been produced as a result of centuries of selection is nowhere better illustrated than by the timely action of the late William Saunders (fig. 9), then superintendent of gardens and grounds of the United States Department of Agriculture, Washington, D. C.

Figure 9.—William Saunders (1822–1900), superintendent of gardens and grounds of the United States Department of Agriculture at Washington, D. C., through whose efforts the Bahia navel orange was successfully introduced from Brazil in 1870. Three years later trees propagated by Saunders were planted in California and, under the name of Washington Navel, became the basis of an epoch-making industry.

In 1870, through the kind assistance of a missionary stationed at Bahia, Saunders imported from Brazil 12 navel orange trees in tubs. These were housed in the Department greenhouse at Washington, and propagations were made for distribution to the regions adapted to citrus culture. The first propagations were sent largely to Florida and California, but at least one of this lot is still maintained by the Department at Washington. Mr. and Mrs. Luther C. Tibbets were attracted to the settlement at Riverside, Calif., and early in 1873, before starting her journey, Mrs. Tibbets visited the Government propagation gardens at Washington, where Mr. Saunders gave her two Bahia navel trees. These were carried to California and planted beside the Tibbets' cottage in Riverside (fig. 10). In February 1879 the fruit was awarded first prize over other navels exhibited from Orange County, and these two trees were used as the source of extensive plantings. The variety was referred to as the Washington Navel to distinguish it from the Australian importations. An attempt was made to change the name to Riverside Navel, but this proved

unsuccessful. The great superiority of the Washington Navel (fig. 11) was soon recognized, since it apparently was ideally adapted to the climatic and soil conditions of California and produced a fruit of high quality with the highest market appeal. The best strain of Washington Navel, according to Shamel and associates (*61*), is characterized by an—

> open and somewhat drooping habit of growth and dense foliage with large, oval, dark-green leaves. * * * Under normal conditions no pollen is produced by the anthers of the flowers. * * * The fruits * * * are obovoid in shape and generally of medium to large size. The rind is of medium thickness, and the texture is smooth and grained. The color of the fruit is bright orange; the rag is tender and comparatively small in quantity; the juice is abundant and of superior quality, having a pleasing and sprightly subacid flavor. The fruits are seedless, and the navel usually is small, sometimes rudimentary, with no development except in the rind.

By 1885 enterprising nurserymen had introduced most of the important varieties of the world, which were tested in comparison with the local seedlings of special merit. Less profitable varieties were rapidly eliminated, and by 1900 the area planted to the Washington Navel was larger than that of all other varieties in the State. It is now generally recognized that one of the outstanding events in the economic and social development of California was the introduction of this orange in 1873. During the period of more than 60 years following, a great industry has been built up from the two small trees planted by Mrs. Eliza Tibbets.

The Valencia variety of sweet orange, introduced into California and Florida between 1870 and 1872 as already detailed, is the other outstanding orange variety in the State. These two varieties are grown almost to the exclusion of others. Climatic conditions vary widely because of differences in rainfall, protection by mountain ranges, the moderating influence of the ocean, and other factors. These affect the ripening period of fruit varieties so that the same variety matures at different times in various regions. When this is coupled with "tree storage" in the case of the Valencia, which holds its fruit in good condition for several months, the combination results in a marketable fruit crop throughout the year. This tree storage is made possible by the dry summer climate with comparative freedom from fruit-destroying fungi, together with other climatic factors contributing to a long ripening season. The movement of Washington Navels begins in November and ends in May. The Valencia crop is marketed from May to November and, as a rule, overlaps by several weeks the period when navels are shipped.

Frost (*21*) reports that the Citrus Experiment Station of the University of California, at Riverside, has recently introduced a good early nonnavel variety, Trovita, which has pollen and a few seeds. This variety originated as one of three seedlings grown from Washington Navel seeds accidentally found. It is pointed out that this may be a promising variety in the hotter citrus districts because of its seeding tendency, since the seedless Washington Navel often fails to set fruit under these conditions. The fruit of the new variety is much like that of Washington Navel, but the navel structure is usually absent or rudimentary.

Figure 10.—Tree of the Washington Navel orange at Riverside, Calif., the lone survivor of the original budded trees of this variety sent to California in 1873, propagated from the introduction made in 1870 from Bahia, Brazil, by William Saunders, Washington, D. C. A tablet in memory of Mrs. Eliza Tibbets, who first planted this navel orange and brought it to fruiting, stands near the tree.

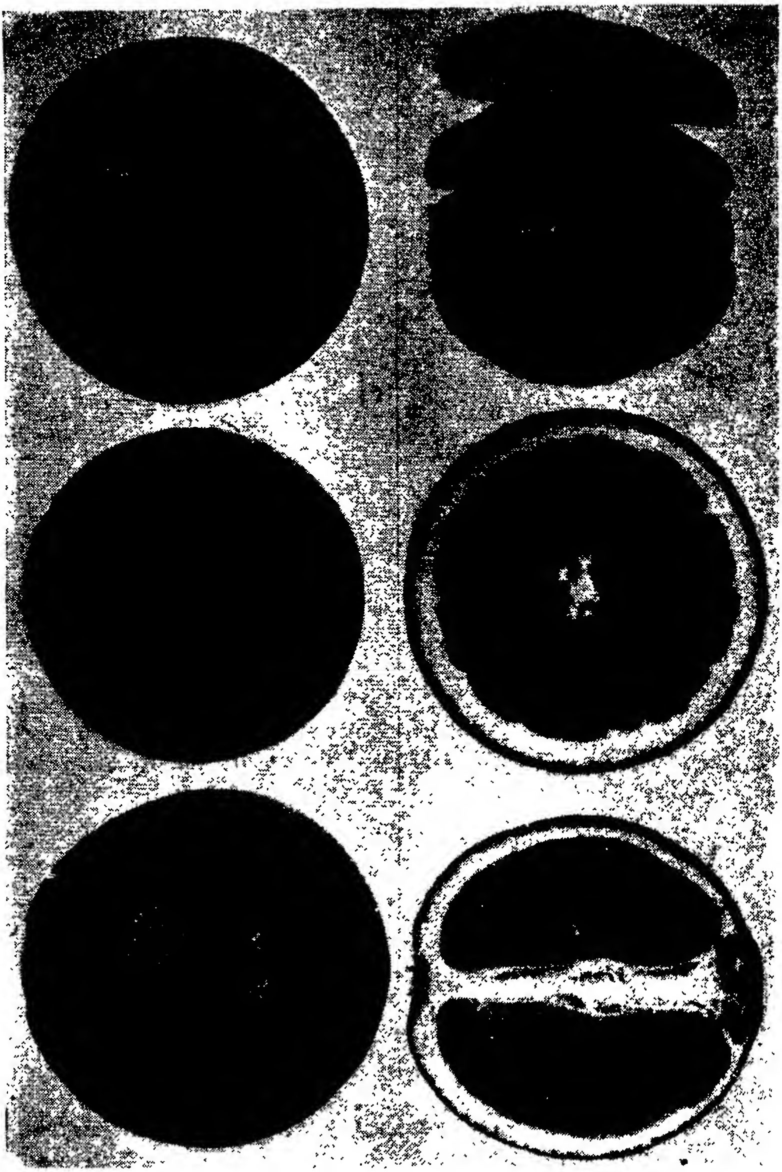

Figure 11.—Washington Navel orange fruit, typical of the variety as grown at Riverside, Calif., showing solid but juicy pulp, locules separating easily, firm, rather thick rind, small navel, and absence of seeds.

Texas

The commonly grown varieties of sweet oranges, along with other varieties of citrus, were brought into the lower Rio Grande Valley of Texas early in the twentieth century, but in general these are not as

well adapted to the climate as the grapefruit. The most desirable early to midseason variety of orange is the Hamlin. The trees are prolific, regular bearers under lower Rio Grande Valley conditions, maturing their fruit in October. Although the Pineapple is the most widely planted early variety, the Weslaco substation of the Texas Agricultural Experiment Station recommends that Hamlin and Joppa should replace varieties such as Pineapple, Parson Brown, and Ruby, which are characterized in Texas by the production of undersized fruit and by erratic bearing habit (*16*). Even the desirable strains of Washington Navel are not satisfactory, being "rather erratic in their bearing habits" and producing juice "variable in flavor, often being quite insipid (devoid of acid)." A recent introduction, one of several navel oranges brought by the Department from Brazil and now under test at the Weslaco substation, is very promising. It has been named Texas Navel (fig. 12) and is being tried extensively by growers. The tree is vigorous and somewhat more productive than the strains of Washington Navel under Texas conditions. The fruit is typically navel in structure, of medium size and good quality.

The Valencia, which matures its fruit from December to January under lower Rio Grande Valley conditions, is the "most profitable commercial variety at the present time, since the trees are productive and fairly regular in bearing, but a large proportion of the fruit, which are of good quality, is undersized."

The Temple orange, which belongs to the horticultural group of high-quality hybrid fruits (tangelo oranges) and is similar to the sweet orange, is promising under Texas conditions, but the rind texture is unattractive and the tree is not hardy. In this same group the Orlando, Seminole, Minneola, and Umatilla varieties are under test.

As far as the standard varieties of sweet oranges are concerned, none is entirely satisfactory under lower Rio Grande Valley conditions.

Louisiana

In the extreme southern tip of Louisiana on the Delta of the Mississippi, south of New Orleans, in the vicinity of Buras, a type of high-quality nonnavel sweet orange of local origin has been grown for a great many years along with some navels of recent introduction. The annual output is usually about 300 cars, marketed primarily in New Orleans.

Grapefruit Improvement

The origin of the grapefruit as a horticultural citrus type is obscure. It is apparently intermediate between the large acid shaddock and the mild salad citrus type commonly referred to as the pummelo. It was brought to Florida from the West Indies and does not correspond to any type in the Orient. It was not appreciated until it was brought to the attention of the consuming public in the 1880's by enterprising Florida citrus growers. It represents a most important horticultural achievement, for it is now found on the breakfast table in either the fresh or the canned state not only in the United States but also in Europe, South Africa, and Australia.

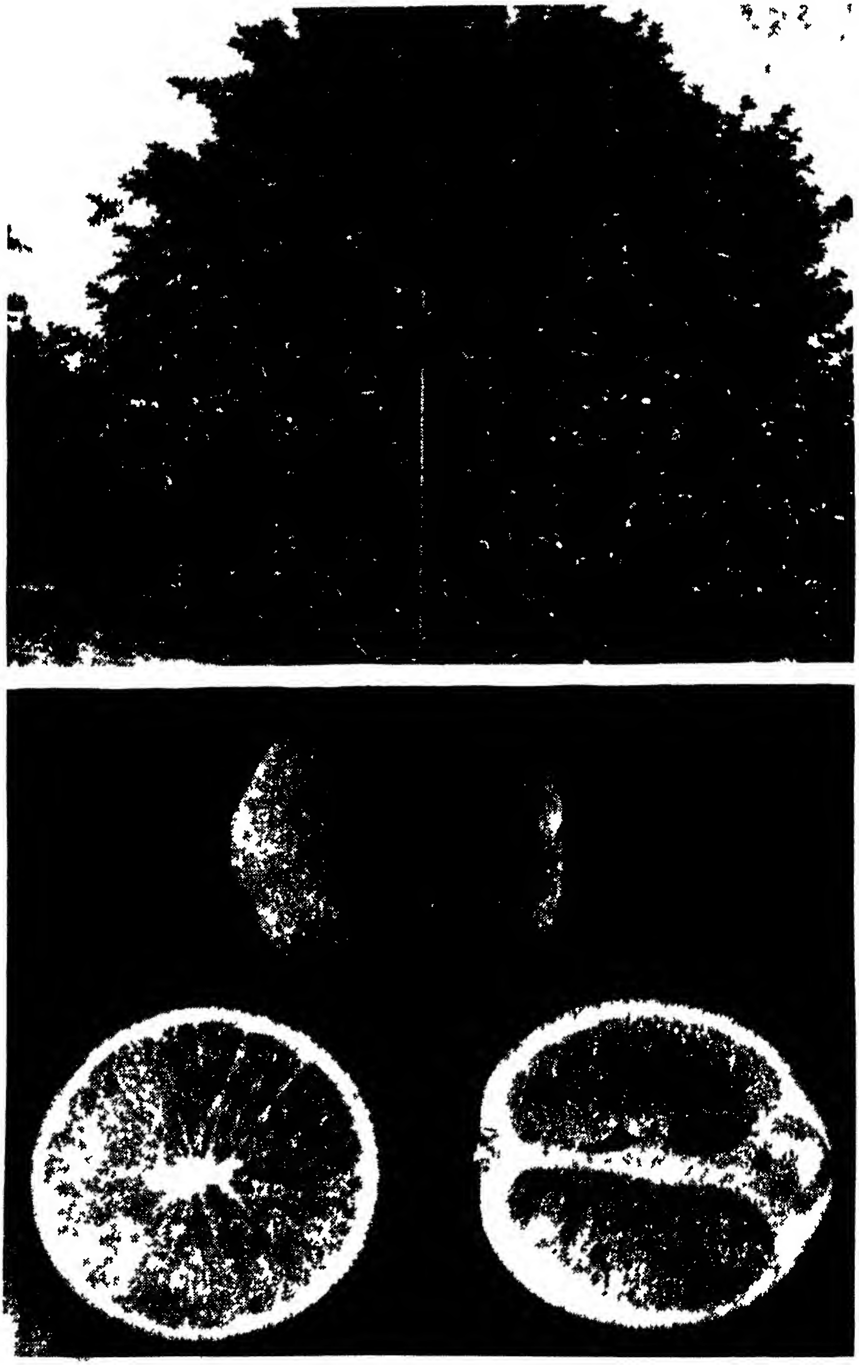

Figure 12.—See legend on opposite page.

Florida

The grapefruit industry in Florida was founded originally on seedling trees, which are very much like the Duncan variety in structure and quality and are now known as Florida Common. The original Duncan tree, over 100 years old in 1926, according to Hume (*32*), was still living in the planting known as the Snedicor Grove near Green Springs, in Pinellas County, where it originated as a seedling from a grapefruit tree grown by a Spanish settler, Don Philippe. Later reports are not available. Duncan (*14, p. 136*) stated in 1892 that Don Philippe brought grapefruit and orange seeds from Cuba 50 years previously and made his planting at Safety Harbor in "Philippe Hammock", and that the orange trees died out from neglect while the grapefruit trees remained in a thrifty condition. The variety was introduced and propagated by A. L. Duncan, of Dunedin, about 1892. It is a very superior variety. Although 17 or more main varieties were later introduced, Duncan remained the favorite among the seedy varieties. Duncan and other seedy varieties are now being top-worked to Marsh in some instances because of the demand for a seedless fruit.

Figure 13.—Egbert N. Reasoner (1869–1926), pioneer nurseryman of Florida, active in the introduction and propagation of many subtropical fruits. He introduced Foster, Thompson, Pernambuco, and Royal grapefruit varieties and the Oneco tangerine, initiated the commercial propagation of the lychee, and was active in testing and disseminating new varieties of mangoes and avocados.

Because of its seedlessness and other desirable qualities the Marsh variety has been gradually replacing the seedy varieties in plantings within the last 15 years. This variety originated in the William Hancock grove at Socrum, near Lakeland, and was first cataloged by C. M. Marsh in the Catalogue of the Lakeland Nurseries for Fall 1896 and Spring 1897, with the statement that the parent tree was a seedling that had been a prolific bearer for 30 or 40 years. Propagation evidently began some years before, as the parent tree was killed in the freeze of 1894–95. A story receiving credence in

Figure 12.—The Texas Navel orange. *A*, Tree showing vigorous habit of this navel variety, an introduction from Brazil made by the United States Department of Agriculture in 1917 when the Washington Navel proved poorly adapted to lower Rio Grande Valley conditions. The tree has a height of 20 feet and a spread of 21 feet. *B*, Fruit of the Texas Navel orange, which resembles the standard Washington Navel in physical characteristics and quality but is more prolific under conditions in southern Texas. Fruits average 2¾ inches in diameter.

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recent years that the variety originated as a broken root sprout from a common seedy type tree has been definitely disproved by the testimony of members of the Hancock family and other local residents who were thoroughly familiar with the original seedling tree (*56*).

The Marsh variety has given rise to two pink-fleshed bud mutations. A. D. Shamel has described one of these that originated near Riverside, Calif., and was brought to his attention in July 1919 by L. V. W. Brown. The mutation that occurred in Florida, in the grove belonging to W. B. Thompson near Oneco, was discovered by S. A. Collins and introduced under the name of Thompson by Reasoner Bros. (fig. 13), of Oneco, in 1924 (*55*). Both of these mutations are identical with Marsh except in flesh color. The Thompson variety, although not extensively planted in Florida, has become an important variety in the lower Rio Grande Valley of Texas.

The Foster, another pink-fleshed variety, originated as a branch mutation on a tree of the Walters grapefruit. This occurred in the Atwood Grove near Palmetto, and was first observed in the season 1906–07. It was named and introduced by Reasoner Bros. in 1914. Aside from the color, the fruit has much the same quality as the parent variety, though it is sometimes regarded as earlier maturing. The color of the pulp, as well as that of the Thompson, tends to fade as the fruit reaches full maturity.

Another seedless grapefruit, the Davis, originating from a cross between a seedling type of grapefruit and a tangerine (in the attempt by Department workers to secure a tangelo) is receiving favorable attention. In shape and size it resembles the Marsh, though it is more rounded in form, but it has the taste quality of the seedy grapefruit, with apparently less glucosidal flavor than the Marsh. Its outstanding character, however, is the fact that it has proved satisfactory for canning, the pulp remaining firm, while the Marsh tends to become soft from processing (*34*).

In the improvement of grapefruit there has been a steady trend toward the use of fewer varieties, and Marsh, largely because of its seedlessness, has become the standard for new plantings, gradually superseding the 17 or more other varieties—Aurantium, De Soto, Excelsior, Hall, Josselyn, Leonardy, Manville, May, Bowen, McCarty, McKinley, Inman, Pernambuco, Royal, Triumph, Walters, etc.

Texas

The Florida grapefruit varieties were introduced into California, Arizona, and the lower Rio Grande Valley of Texas.

The grapefruit is apparently well adapted to the lower Rio Grande Valley, and it has served as the basis of a citrus industry built up since 1910. As grown in the valley it has "a pleasing, mild flavor that has met with favor in most of the markets where the fruits have been offered for sale" (*16*).

Such varieties as Duncan, Conner, McCarty, Inman, and Walters, all seedy varieties, are grown to a limited extent for the early market, but they are at a discount after the seedless variety, Marsh, is ready for market.

The pink-fleshed varieties Foster (seedy) and Thompson (seedless) have pink flesh early in the ripening season and usually sell at a

premium. The Ruby, a local mutation from Thompson, has both pink flesh and pink rind and is receiving some attention in recent plantings.

California and Arizona

The grapefruit industry in the Southwest began after the introduction of the Marsh grapefruit in 1890; the plantings of other varieties previous to that time did not prove profitable. In the Arizona citrus districts and in the Coachella and Imperial Valleys of California, grapefruit matures fairly rapidly and is marketed in late fall and early winter; in other California grapefruit districts it does not reach full maturity until the following spring or summer.

Mandarin Improvement

In the mandarin orange group the tangerine and satsuma oranges are grown to supply special markets, primarily early in the season. The chief breeding problem is in connection with the production of high-quality early-maturing varieties.

Tangerine Orange

The only variety of tangerine orange extensively planted in Florida is the Dancy, a prolific variety that was originated as a seedling by George L. Dancy, of Buena Vista, St. Johns County, and was introduced in 1871 or 1872. This variety is of great interest, since it is the pollen parent of most of the tangelo oranges, and it imparts to the best tangelos the deep orange rind and flesh color and the aromatic and pleasing ester qualities. In Texas, although the earlier plantings are mostly Dancy, the Clementine (Algerian) is decidedly superior to this variety, as is also the Warnuco (Ponkan) under lower Rio Grande Valley conditions.

In California the Dancy is grown to a limited extent for special markets, but apparently the small size and higher acidity developed when it is grown in this section has retarded extensive planting. Recently three mandarin varieties, developed by Frost (*21*) at the Citrus Experiment Station, Riverside, have been introduced for preliminary trial. They were originated as a first-generation cross between the King orange and other mandarin oranges. In the case of the Kara, the Owari satsuma was the seed parent, and in the case of the Kinnow (fig. 14) and Wilking, the King orange served as the seed parent and the Willowleaf mandarin was the pollen parent. These varieties produce fruits of good size and excellent quality, but, as pointed out by Frost, only orchard tests can determine their ultimate value in citrus culture.

Satsuma Oranges

The satsuma orange was first introduced into Florida by George R. Hall in 1876. In the upper Gulf coast region, from western Florida to eastern Texas, it has been grown commercially since 1910, and the industry is based primarily on the Owari satsuma. Although there are apparently two or more strains of this variety, they do not differ widely. The fruit is harvested early in the season, October and November. It is desirable to harvest as early as possible for two reasons—to secure the early market before many high-grade sweet

oranges are shipped from peninsular Florida, and to remove the fruits early enough to allow for the storage of maximum food reserves in the tree before the onset of winter. In an attempt to meet this need, the Department of Agriculture imported over 50 strains of the early-maturing satsuma from Japan, and these are under test at the Gulf Coast Substation at Fairhope, Ala., in cooperation with the

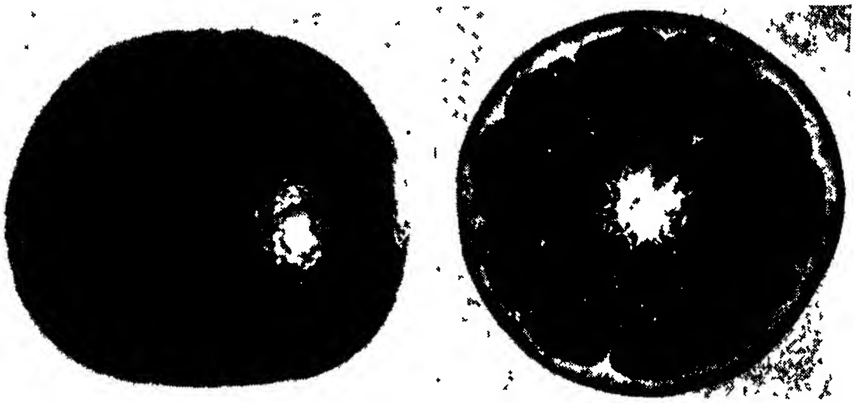

Figure 14.—The Kinnow mandarin, a hybrid of King orange and Willow leaf mandarin, the King serving as the seed parent. The fruit is excellent in appearance and flavor, remaining firm when fully ripe; desirable for local consumption but shipping quality undetermined. Fruits shown are natural size, about 4½ months after ripening. Introduced by Frost, of the California Agricultural Experiment Station.

Alabama Agricultural Experiment Station and with growers in various parts of this section. So far the Kawano variety has shown some promise, but it does not uniformly mature earlier than the Owari. Some of the other strains may prove more regular in this respect.

A selection from extra vigorous apogamic seedlings following cross-pollination of the satsuma orange with the sweet orange is promising from a commercial standpoint. The Silverhill variety, originated in this manner, has now been tested for a number of years and appears to be a superior strain of the Owari. It has shown somewhat more resistance to cold than the other satsuma varieties, but the evidence is not conclusive.

Improvement of Acid Citrus Fruits

The chief center of lemon culture is in California, and lime production is confined primarily to Florida.

Florida

The introduction of the citrus scab proved a serious drawback to lemon culture in Florida. There is also great difficulty in properly curing lemons in the humid summer climate. In 1931 the Department introduced the Perrine lemon (fig. 15), a hybrid between the Genoa lemon and the Mexican or Key lime. It is highly resistant to citrus scab and anthracnose and has given a new impetus to the industry.

The Perrine lemon is a rapid-growing, vigorous, and productive tree. The fruits are borne singly or in clusters and are of medium size, with a high acid percentage, ranging from 6.2 to 7.2 percent, ranking with standard commercial varieties in this respect (*71*, *80*).

The Meyer lemon, an introduction from China named for the introducer, the late Frank N. Meyer, famous plant explorer for the Department of Agriculture, is chiefly noteworthy for its frost resistance.

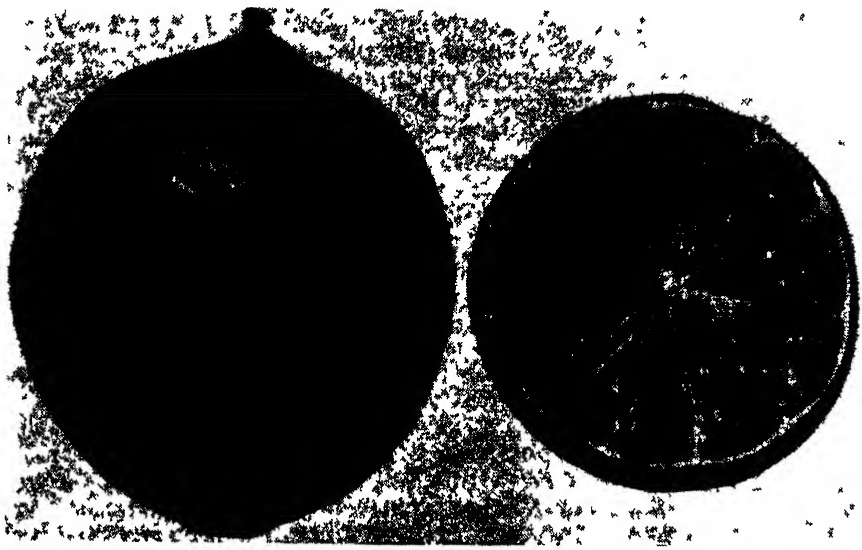

Figure 15.—Typical fruits of Perrine lemon, a hybrid between the lemon and the lime; remarkable for its resistance to scab and anthracnose, vigor of growth, and heavy bearing. Resembles the true lemon in shape, size, and acid content. Introduced by the United States Department of Agriculture.

Its low acid content (4.3 to 4.8 percent), large size, and round shape preclude its general popularity as a commercial lemon, though it is well suited to local needs where true lemons have proved too tender

The Key, Mexican, or West Indian lime has long been cultivated primarily on the keys, but recently the industry has declined because of hurricane damage. The Tahiti (also called Persian or Bearss) lime has recently been planted to a considerable extent in Dade County and the southern ridge section. It has high quality, and in addition the aromatic properties of the rind are highly valued by the consumer The Lakeland and Eustis limes, hybrids of lime and kumquat, introduced by the Department, although of high juice quality, are of small size and have a thin rind, which may prove disadvantageous for storing and shipping.

California

In the early development of the industry a large number of European varieties of lemon were grown and also many seedlings were raised, most of which were not promising. The present plantings are practically limited to Eureka and Lisbon. The former originated from a seed planted in 1870 by C. R. Workmen in Los Angeles. The Lisbon

variety originated in Europe. Shamel and coworkers (*64*) state that the Lisbon lemon was introduced into California in a number of importations, the first of which was made as budded trees in 1874 and 1875 from Australia. It has been pointed out that the advantages of the Eureka are its comparative freedom from thorns, its tendency toward early bearing, and its prolific bearing qualities. The tendency to bear fruit on the tips of the branches and the inclination to grow long canes with but few laterals and to drop its leaves on the long canes or branches, leaving the limbs and fruit too much exposed to the hot rays of the sun, are disadvantages.

The Lisbon has heavy foliage, which protects the fruit from sunburn, and the fruit is borne uniformly throughout the tree. This variety has a tendency to bear one large crop maturing in winter, with only a small amount of summer fruit.

MINOR CITRUS FRUITS

In the United States the pummelo, citron, kumquat, and sour orange are not grown to any appreciable extent for their fruits. Of these minor citrus fruits the pummelo is the most promising. The citron is grown mainly for exhibition purposes, although a beginning has been made in California with preserving it on a commercial scale. The sour orange is grown as an important marmalade fruit in some other citrus-producing countries, notably in Spain

The pummelo in its better varieties is a most delicious salad citrus. The juice does not possess the sprightly acid and naringin (bitter) properties of the grapefruit, but when the juice sacs are served as a salad the inimitable flavor is relished by all who have had the good fortune to sample them. In times past only the sour shaddock was known in the citrus-producing districts, but since 1915 the Department of Agriculture, through its collaborator, G. Weidman Groff, in China, has introduced an important collection of pummelos. These are not as yet well known but are being distributed to those interested in the culture of the fruit. One of the outstanding varieties is named Siam. Reference to this collection will be found in table 5.

The Department has also imported a valuable collection of citron varieties, including practically all of the important ones. Corsican, the chief variety of commerce, was one of the first citrus introductions made by Fairchild, who was for many years in charge of the plant introduction work of the Department.

Kumquats were introduced into Europe as recently as 1846 by Robert Fortune. Importations into the United States were made by Taber in 1885 and Reasoner in 1885 and 1890. The varieties Nagami (oval) and Marumi (round) were first introduced, and later the Meiwa or sweet kumquat. The Nagami predominates in all plantings made thus far. About 1910 the Department introduced the Hong Kong or wild kumquat, which produces very small round fruits and is of interest from the breeding standpoint in that it has the double haploid chromosome complement. (See the later section on cytology in this article.)

The Department has introduced a superior variety of sour orange named Oklawaha. It originated as an apogamic seedling when pollen of the shaddock (sour pummelo) was used to pollinate the sour orange.

In habit the tree appears as a vigorous sour orange. The fruit is similar to the ordinary sour orange but averages larger in size, 3 to 4 inches in diameter, and it is superior to the ordinary seedling sour oranges as a marmalade variety.

CITRUS BUD SELECTION

WITH the general acceptance of De Vries' mutation theory (1901), the improvement of varieties by the selection of bud mutations soon became a recognized mode of procedure in plant breeding. Conversely, the elimination of inferior bud mutations became of equal or even greater importance in many clones especially subject to mutations.

That the Washington Navel orange is subject to bud mutation was recognized at an early date, and by 1910 the problem was so serious that at the California State Fruit Growers Convention of that year Coit (*10*) proposed to "keep individual tree records for 2 years and these trees with records to be offered nurserymen for propagation as pedigreed trees." At the same meeting Coit, in discussing the application of the De Vries mutation theory to the problem, said:

> If you go out into the average navel orchard to select a dozen perfect navel oranges true to old standards, you will be surprised at the amount of searching necessary. * * * It is my belief that by far the greatest part of the divergence is attributable to mutation * * *.

He added that propagators—

> must be quick to see and cut out all branches sporting toward poor types. In the second place, we must be exceedingly careful in cutting budwood. * * * Select buds from those branches which produce your ideal of the navel orange.

The problem was so serious that the Department of Agriculture detailed A. D. Shamel to study it in 1909, and he began his work in cooperation with the California Citrus Experiment Station at Riverside and with citrus growers. In his first report entitled "Bud Selection in Citrus Fruits", given at the California State Fruit Growers Convention at San Bernardino, March 8, 1911, Shamel set forth the problem clearly. His work began with the Washington Navel and was extended to include other sweet oranges, the lemon and grapefruit types, as well as other crop plants.

Over a period of 27 years the work of Shamel and his coworkers (*57, 58, 59, 60, 61, 62, 63, 64*) has been characterized by consistent, painstaking research, which has included a study of the source of strains originating as bud mutations and unintentionally propagated by nurserymen and growers. This was followed by efforts to eliminate the inferior trees in established plantings by top-working with carefully selected buds. Further efforts were made to avoid the propagation of undesirable strains arising from bud mutations by systematic selection on the basis of individual plant performance and an intimate knowledge of the plants. Finally, a systematic search was made in cooperation with growers for superior plants originating from commercially valuable bud mutations, and these were tested in progeny plantings to single out the ones inherently superior to the parent forms for utilization by the industries concerned.

In the case of Washington Navel orange it has been shown (*61, p. 67*) on the basis of individual performance records made in several California groves since 1909 that—

these groves consist of at least 20 strains of commercial importance with five or more others of less economic consequence. The trees of each of these strains have fruit or vegetative characteristics, or both, which serve to distinguish them from all other trees of the variety.

About 25 per cent of the total number of trees studied in the original orchards in which these investigations have been conducted were found to be of undesirable strains having consistently low yields, or bearing fruits of poor quality, or both, such as those of the Australian, Unproductive, Corrugated, Pear-Shape, Sheep-nose, Flattened, Dry, and other inferior strains.

The extent of the commercial use of superior strains selected for the production of more uniformly good fruit is indicated by the sale of selected buds by the Fruit Growers Supply Co. for the period 1917–35. These data, given below, include only a part of the supplies of such buds used by nurserymen and growers-- probably not more than 50 percent; but because they are conservative they will the better convey some idea of the value of this kind of work.

Name of strain	*Number of buds sold*
Superior strain of the Washington Navel orange	1, 402, 950
Superior strain of the Valencia orange	2, 338, 004
Superior strain of the Marsh grapefruit	1, 262, 757
Superior strain of the Eureka lemon	766, 950
Superior strain of the Lisbon lemon	86, 215
Superior strains of miscellaneous citrus varieties	66, 886

Two special citrus strains originating as bud mutations, the Robertson Navel orange in 1925 and the Dawn grapefruit in 1929, are now being introduced, and the indications are that they will be widely grown in certain citrus districts of California and Arizona. In the Robertson Navel orange strain the fruits are resistant to June drop on account of their very rapid early growth. They mature about 1 month earlier than those of the Washington Navel orange under comparable conditions, and the trees are more productive than the normal Washington Navel. Otherwise the mature fruits of the Robertson strain and those of the parent variety are very similar and cannot be distinguished even by those who have grown and studied them.

The Dawn is a strain of the Marsh grapefruit in which the fruits mature about 1 month earlier than those of the parent variety, and the trees are unusually productive. Otherwise the Dawn and the Marsh trees and fruits have similar characteristics. The indications are that this strain will be a particularly valuable one for growing in the desert grapefruit-growing districts.

Many other citrus bud mutations are under test in cooperation with growers in California and Arizona, and some of these promise to be of commercial importance in the near future.

In the history of subtropical fruit breeding the work of Shamel, his coworkers, and the California Agricultural Experiment Station cooperators is inspiring. It is characterized by consistent, painstaking research and unwavering purpose. In the earlier years, although the work was fully appreciated by the growers in the region, scientific workers elsewhere did not give entire credence to the remarkable evidence uncovered. As time went on, Shamel and his coworkers answered their critics by applying statistical methods to the data, which gave convincing proof of the conclusions. Later, numerous bud mutations were also discovered in other fruit types, including apple, and by the time the work was no longer challenged the results

achieved stood out as monumental in this particular field of research. The practical benefits to the industry can be gaged by the millions of selected buds that have been used by the citrus growers in California and elsewhere. A summary of the bud mutations and strains isolated by Shamel and his coworkers is to be found in table 8.

In Florida a bud-selection project has been in progress since 1921. The mode of procedure differs somewhat from that followed in California and was developed cooperatively by the Florida Agricultural Experiment Station and the Department of Agriculture. At the Lake Alfred Citrus Experiment Station a progeny grove has served as the basis of variety improvement. In this progeny grove standard varieties of oranges and grapefruit are represented by rows budded from parent trees of known production, several such selected parents being included for each variety. Production records have been kept, and a detailed study of fruit characteristics has been made as the basis for reselection among the original progenies. For purposes of comparison a few offtype progenies have been included, which have served well to illustrate the importance of careful bud selection in nursery propagation. Growers and nurserymen have gradually come to realize the value of such true-to-type budwood, which has been made available through the experiment station for several seasons past at a cost not greatly in advance of common commercial rates.

Other bud mutations of value to the citrus industry are Foster, Thompson, Ruby, and Davis grapefruit (described above), Silverhill satsuma orange, and Oklawaha sour orange, the three latter being seedling or nucellar mutations

ROOTSTOCKS

A NUMBER of citrus types and varieties are of major importance because of their value as rootstocks for the varieties grown commercially. In the early development of the citrus industry, especially in Florida, seedling citrus trees were extensively planted, but gradually this practice was discontinued, as it was realized that certain rootstocks were better adapted to the soil conditions. This advance was made by the expensive trial-and-error method, and the stage reached by the 1890's was recorded by Van Deman (*81*). Planned experiments with rootstocks have been relatively rare. In California, Mills (*46*) has reported results secured at the experiment station at Pomona, and Bonns and Mertz (*3*) described the experiments carried out at the Citrus Experiment Station at Riverside. The important work of Webber (*85*) at the citrus station is an illuminating piece of research into the seedling variation of the types commonly used as rootstocks. Unfortunately, the work of Taber (fig. 16) quoted by Hume (*31, pp. 209–218*) at the Glen St. Mary Nursery in Florida was discontinued too soon. Traub and Friend (*77*) have reported on preliminary experiments in the lower Rio Grande Valley of Texas. Akenhead, Feilden, and Hatton (*1*) have recently summarized the investigation on citrus rootstocks.

As indicated, the horticultural utilization of rootstock types is based at present mainly on the knowledge accumulated through many years of trial and error. The final results are very valuable, though they were secured at great economic expense. The entire field has not been exhaustively explored.

In general it may be stated that in Florida, as pointed out by Camp (4), the rootstock problem is more complex than in the lower Rio Grande Valley of Texas, in California, or in Arizona.

Three major considerations are necessary in the choice of suitable rootstock—congeniality between stock and scion, resistance to diseases, and adaptation to the soil and climatic conditions. Rootstocks have been tested over a considerable period by commercial growers, and at the present time only three are extensively used—sour orange, rough lemon, and the trifoliate orange. The Cleopatra mandarin has recently received some attention as a rootstock. In Florida, trees on grapefruit stock grow vigorously in the early stages but usually prove to be shy bearers and show decline after a number of years. Sweet orange is susceptible to foot rot, and both grapefruit and sweet orange are less cold-resistant than sour orange. The commercial lemon is susceptible to diseases, and trees on it are short-lived. The citrange has been tried as a substitute rootstock in place of the trifoliate orange for the satsuma orange, but recent observations have shown that the citrange is not reliable in the Gulf coast region, since it is evergreen and does not go dormant sufficiently during the winter season. This has resulted in the loss of the scion variety in some seasons.

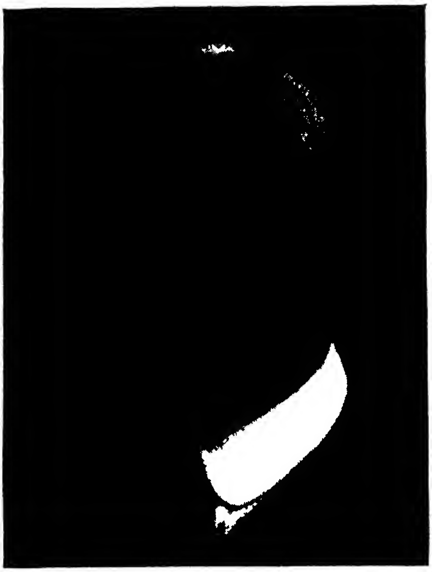

Figure 16.—George Lindley Taber (1854–1929), pioneer nurseryman of Florida, who demonstrated the limitation of the satsuma orange to trifoliate orange stock, founding a new industry; introduced Duncan grapefruit, Lue Gim Gong sweet orange, and varieties of persimmons, and cooperated with the United States Department of Agriculture in the production of early citrus hybrids.

The sour orange is a useful stock in all citrus-growing regions except South Africa, where all attempts to use it so far have failed. It is compatible with most citrus types except satsuma, kumquat, and lime. In California, lemon trees on this stock may show decline after 10 to 20 years, which has been attributed to the stock. For this reason many of the recent lemon plantings in California have been budded on the sweet orange. The sour orange is highly resistant to cold and to root and crown bark diseases, but highly susceptible to citrus scab. Roots are deeply penetrating, and the stock is well adapted to clay subsoils and wet or heavy soils. In Florida it is successful on moist hammock as well as on moist flatwoods soils and on the heavier soil types in general. In California, Arizona, and the lower Rio Grande Valley of Texas it tolerates irrigation conditions. This, together with its adaptability to southwestern conditions, has made it the rootstock almost universally used in these regions. Its

main drawback is its relatively slower growth on light soils as compared with rough lemon, but on heavier soils the rate of growth is satisfactory.

The rough lemon (*Citrus limonia*) makes a satisfactory growth even on very light and sandy soils. This makes it valuable in certain sections of peninsular Florida. It is highly susceptible to citrus scab and susceptible to foot rot and other root and crown diseases, but this apparent handicap is minimized, for on sandy soils these diseases are less troublesome than on the heavier ones. It is extensively used as a rootstock for citrus on soil types not suitable for sour orange in Florida. It is not well adapted for use with the satsuma orange, producing coarse, raggy fruit.

The trifoliate orange was once recommended as a rootstock for citrus in the lower Rio Grande Valley of Texas (*48*), chiefly on account of cold resistance; but it proved susceptible to foot rot and cotton root rot and was later discarded in favor of the sour orange (*77*). In the upper Gulf coast region it is universally used as a root stock, since it is deciduous and goes more dormant during the winter season than evergreen citrus types. It is the hardiest of the citrus types.

Recently the Cleopatra mandarin has been recommended as a rootstock in place of rough lemon, chiefly on the basis that it is more cold-resistant than the rough lemon and tends to produce better textured fruit, holding fruit later in the season in good condition. It is immune to scab and resistant to gummosis. However, experimental work has not been carried out extensively enough to warrant unqualified recommendation.

It has already been pointed out that most citrus seeds produce more than one seedling, and that any extra seedlings not of seminal origin are produced by budding from the mother plant tissue. On the surface it would appear that this is an ideal condition from the standpoint of seedling rootstock production, since it would give a large percentage of plants like the original stock, and this is true in the main. Webber (*85*) and Frost (*20*) have shown, however, that variations may occur even among such nucellar seedlings. Frost points out the influence of mutations in this connection. The work of Webber is of special interest. His experiments, which were started in 1914, show that—

> citrus seedlings of the species and varieties most commonly used as rootstocks exhibit a wide range of variation. In any lot of seedlings grown from seed of the same variety and from the same source, the great majority usually are of the same general type, but from 5 to 40 per cent of them are highly variable types which apparently differ in genetic constitution from the prevailing type and from each other.

These variants may include both apogamic and seminal seedlings. They are usually small and lacking in vigor and when used as stocks induce dwarfing of the tree. His experiments show that small seedlings and "small budlings tend to produce small, low-yielding orchard trees; and that large seedlings and large budlings tend to produce comparatively large, high-yielding orchard trees." In order to secure the desired uniformity in orchard trees, Webber advises "a moderate culling of small seedlings at the seed bed, followed by a careful roguing and destruction of all variants and small seedlings in the nursery just prior to the budding."

CITRUS IMPROVEMENT IN FOREIGN COUNTRIES

This section, like the similar sections in connection with other subtropical fruit crops, is based almost entirely on replies received to the questionnaire dealing with the Cooperative Survey of Plant and Animal Improvement. The information received mainly concerns the present and future objectives of breeders.

Mexico

Citrus studies are carried on at experiment stations of Montemorelos, Nuevo Leon; El Yaqui, Sonora; and Emporio Macuspana, Tabasco. Infestation of fruit by the orange maggot, *Anastrepha ludens* Loew, constitutes the most serious problem. Methods of attack are being studied, but without practical results thus far.

South America

At the Instituto Agronomico do Estado de São Paulo in Brazil, work with citrus under the direction of C. A. Kruge, head of the genetics department, is being confined primarily to the improvement of varieties by bud selection and to the improvement of the sour orange rootstock by making extensive progeny tests. The disease resistance of rootstocks is also being studied.

In Chile no breeding work with subtropical fruits is under way at the experiment stations, but Salvador Ezquierdo at Santiago has for many years introduced varieties of citrus, avocados, etc., to test their adaptability to Chilean conditions.

At the Estacion Experimental de Concordia, Argentine Republic, Signor Ruben Bence Pieres, director of the station, is conducting experiments with citrus which concern the selection of sour orange seedlings, with a view to obtaining strong, vigorous, fast-growing plants. A naturally occurring hybrid mandarin named Malvasio, with a large fruit, fine rind color, excellent quality, and late maturity, is being tested and shows promise of commercial value. The main introduced varieties, which have been selected from a large number and are being extensively cultivated, are the Marsh and Qurian grapefruit and the Valencia and Lue (Lue Gim Gong) sweet oranges. The cultivated area of grapefruit and sweet oranges approximates 5,000 acres, with about half devoted to each type. The main problem that confronts the citrus industry is the ravages of foot rot. Work is in progress for the selection of resistant stocks, as indicated above.

Europe and North Africa

At the Estacion Naranjera de Levante at Burjasot, Valencia, Spain, work has been carried on in sweet orange breeding since 1927 under the direction of Manuel Herero. The work has been confined mainly to selection from open-pollinated seedlings of Washington Navel. Two improved varieties have been selected, one round and the other oval in form. These are being cultivated to the extent of about 375 acres. Hybridization work was begun in 1932 and is being carried on to the second generation after crossing. The crosses made are those between the sweet orange and the mandarin.

A. Biraghi, pathologist, Italian Department of Agriculture, Rome, reports that the chief problem with citrus culture in Sicily is in con-

nection with the disease mal secco, chiefly affecting lemons. Attempts are being made to breed varieties resistant to this disease. Two resistant lemon varieties of unknown origin and not desirable for quality have been found locally, and promising varieties have been imported from India (*2*) and the United States for use in breeding experiments.

At the Superior School of Agriculture, Laboratory of Horticulture, Athens, Greece, P. Th. Anagnostopoulos has gathered together a collection of citrus species for selection and breeding work.

In Morocco, under the leadership of F. Lacarelle, director, and Ch. Miedzyrzecki, geneticist, Experimentation Fruitière et Maraichère, Rabat, citrus fruit improvement is being studied through several methods: (1) Bud selection, (2) hybridization to secure improved varieties and varieties resistant to disease, and (3) selection of stocks. The varieties receiving the most attention are Washington Navel, Valencia Late, and Clementine. A special study of the seed content of the Clementine led to the conclusion that seed production is largely dependent on the proximity of other varieties, especially of mandarin oranges, to furnish pollen to the flowers of the Clementine, self-fertilized flowers being almost seedless (*38*, *39*).

Asia and Malaya

At the Jewish Agency Agricultural Research Station, Rehoboth, Palestine, the experimental work was started by J. D. Oppenheim and is now being continued by Ch. Oppenheimer. The work is confined primarily to improvement by bud selection, which was begun in 1934, and by hybridization, begun in 1933. The first-generation hybrids have not reached fruiting stage. The hybrids are from crosses of the Jaffa orange with other early and late varieties, of the blood orange with the tangerine, and of the sour orange with the sweet lime. The station has gathered together a collection of about 70 citrus varieties.

Theoretical studies are under way on the inheritance of peel thickness in citrus and on the effect of pollination on number of seeds.

At the Imperial Horticultural Experiment Station at Okitsu, Japan, T. Tanakawa is carrying on investigations in bud variation in early- and late-maturing satsuma oranges. Sixty-one late strains and 42 early strains are being tried out. The work was started in 1925 and is still in progress. Citrus hybridization work was begun in 1909.

Tyozaburo Tanaka, professor of horticulture at the Taihoku Imperial University, Taiwan, Japan, is engaged in citrus breeding. Kimijiro Noro, pomologist at the Shizuoka (Japan) Agricultural Experiment Station, has made a collection of 80 bud mutations of the satsuma orange.

At the Department of Horticulture, Lingnan University, Canton, China, G. Weidman Groff, professor of horticulture, and Pui-Man Lei, Qu-Nin Shiu, and A. N. Benemerito, pomologists, have gathered together a comprehensive citrus collection for use in the selection of desirable types of citrus and citrus relatives, particularly from the south China area, with numerous introductions from abroad. Some of the systematic work on this collection has been carried out in collaboration with the United States Department of Agriculture.

R. D. Fordham, deputy director of gardens, United Provinces, Saharanpur, India, reports that citrus rootstock trials are under way, including Khatta (Karna lime), *Citrus limonia*, Sylhet, Bijori, Sadaphal, Jamberi, Bilhari, Galgal, Sweet Galgal, Turanj, and sweet lime.

B. Nazareth, superintendent, Modibag Garden, College of Agriculture, Poona, India, reports that studies of mutations occurring in the principal citrus varieties, Santra Mosambi and Ladoo, have been made, and many well-marked sporting forms have been recognized. Breeding work thus far has been confined to mass selection both for rootstocks and for scion varieties. Collections of scion and rootstock varieties are being made to initiate systematic breeding of fruit crops adapted to different soil and climatic conditions. Attempts at hybridization made in 1912, 1914, and 1918 gave negative results. Polyembryony in citrus has been studied, showing varying percentages, from none in the pummelo to 60 percent in the Ladoo orange. The Marsh (seedless) grapefruit has been introduced for culture in the Bombay region.

South and Central Africa

The Department of Agriculture, Zanzibar, East Africa, is studying local and imported varieties of citrus in a series of plots. This work is being carried out by A. Q. Findley, director.

Australia and New Zealand

At the Department of Agriculture and Stock, Brisbane, Queensland, bud selection of citrus has been practiced for many years and Government certified budwood is available for nurserymen. The chief sweet orange varieties grown are Washington Navel, Valencia, Jaffa, Sabina, and Joppa. The lemon varieties are Lisbon and Villa Franca. The mandarin varieties are Beauty of Glenn Retreat, Emperor of Canton, Scarlet, and Fewtrel Early. The grapefruit variety is Marsh, and Seville sour orange is grown for marmalade. Sour orange and rough lemon rootstocks are used for citrus except that mandarin is grown on mandarin.

At the Department of Agriculture, Division of Horticulture, Melbourne, Victoria, J. M. Ward, superintendent of horticulture, has carried on work in bud selection since 1931, and up to the present one variety has been propagated—a thin-skinned early navel orange, which has not as yet been named. The department also supplies buds of selected strains of the Washington Navel and Valencia to growers and nurserymen. No work in hybridization has yet been carried out.

At the Department of Agriculture, Division of Horticulture, Wellington, New Zealand, J. A. Campbell, director, has gathered together a representative collection of citrus species and varieties for intensive study.

H. Wenholz, director of plant breeding, Department of Agriculture, New South Wales, Australia, reports that citrus breeding is being carried on at the Grafton Experiment Farm and the Hawkesbury Agricultural College with the object of producing "a late hanging navel orange" and a late Valencia of fine texture. A cross has been made between Valencia and a very fine-textured seedling variety.

TECHNICAL PROBLEMS AND RESULTS IN CITRUS BREEDING [4]

PROGRESS in genetic research has been greatly retarded on account of the common occurrence of polyembryony in most citrus types, which makes it necessary to grow to the fruiting stage large numbers of

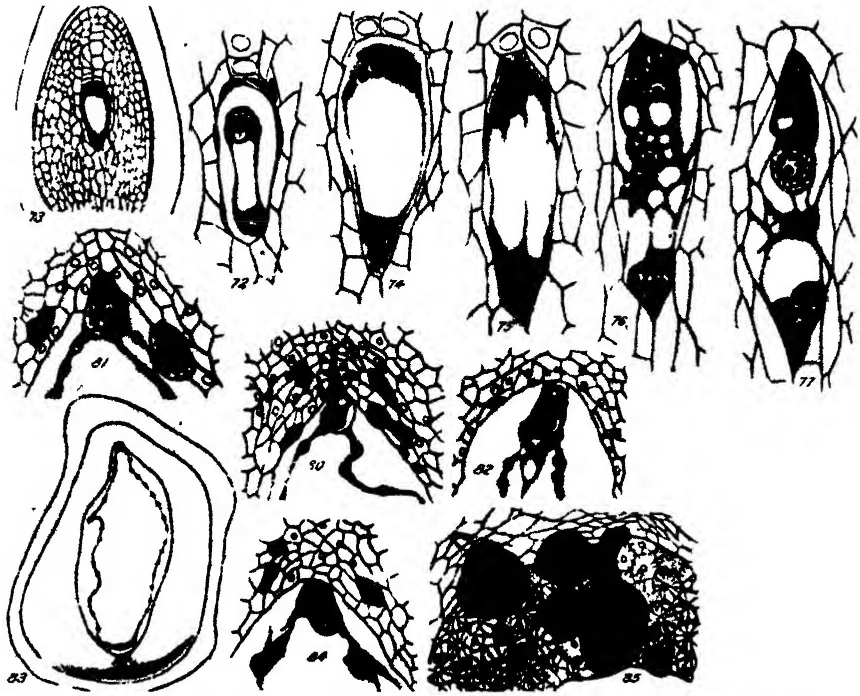

Figure 17.—Embryo development and "nucellar embryony" in *Citrus* and *Poncirus*, after Osawa (*50*): Nos. 72, 80–85, trifoliate orange; 73–76, satsuma orange; 77, Washington Navel orange. (Original magnifications changed to conform to present reduction.) 72, Two-nucleated embryo sac, X 570. 73, An ovule showing embryo sac, nucellus, and inner integument, X 175. 74, Details of embryo sac of no. 73, with four nuclei, X 570. 75, Embryo sac with eight nuclei, X 570. 76, A mature embryo sac with egg apparatus, polar nuclei, and antipodal cells, X 570. 77, The same, X 570. 80, Micropylar portion of an embryo sac, showing fertilized eggs, pollen tube, and endosperm nuclei, especially some large nucellar cells containing large nucleus and much cytoplasm, X 175. 81, The same, X 265. 82, Micropylar portion of an embryo sac showing two-celled embryo and endosperm nuclei, X 175. 83, An older ovule, showing embryo sac, embryo, endosperm nuclei, nucellus, and integuments, X 20. 84, Upper portion of embryo sac of no. 83 more magnified, showing six-celled embryo, endosperm nuclei, and nucellus, X 175. 85, Upper portion of an embryo sac, showing polyembryony, X 370.

seedlings that have arisen asexually. That this section is not more complete is due in the main to this one cause. Even the grouping of citrus species (*68*) is complicated by this condition.

[4] The following sections are written primarily for students and others professionally interested in genetics or breeding.

Cytological Basis for Citrus Genetics

A study of the chromosome numbers and chromosome behavior in citrus is basic to a consideration of citrus genetics. According to Frost (*20*), it may be assumed that bud-variation types originate primarily either as gene (point) mutations or as chromosomal aberrations, and an understanding of these fundamental facts may also throw some light on the great variability of F_1 hybrids between species.

Figure 18.—Howard B. Frost, associate plant breeder, California Agricultural Experiment Station, since 1912, has made important contributions to the cytology and genetics of citrus and is the originator of the Kara, Kinnow, and Wilking mandarins and the Trovita sweet orange.

Strasburger (*66*) determined the haploid chromosome number as 8 in the sweet orange (*Citrus sinensis*), the sour or bigarade orange (*C. aurantium*), and the citron (*C. medica*). Osawa (*50*) reported that the haploid chromosome number in the satsuma orange (*C. nobilis* var. *deliciosa*) was probably 8 (fig. 17).

In 1924–25 both Frost (fig. 18), at the Citrus Experiment Station, Riverside, Calif., and Longley, of the Department of Agriculture, reported important work on the cytology of citrus. Frost (*18*) determined the chromosome numbers in two varieties of sweet orange (*Citrus sinensis*) and one variety of grapefruit (*C. grandis*), and in each case the haploid number was 9. He observed neither polyspory nor polycary.

Longley (*45*) made chromosome counts in 24 citrus species and citrus relatives and verified the basic chromosome number of citrus as 9, but he also found 1 tetraploid species, the Hong Kong kumquat (*Fortunella hindsii* (Champ.) Swingle). He observed both polyspory and polycary in many forms. He states that "irregularities in chromosome pairing at diakinesis and in their distribution at meiosis were frequently noticed. The outcome of such irregularities was the presence of tetrads containing more than the expected four pollen grains." In grapefruit, limes, and limequats polyspory was often observed. He points out that there may be "a relation between irregular chromosome numbers and the production of citrus with supernumerary chromosomes." According to Longley, two factors, however, may hinder the spontaneous appearance of such polyploid forms—the possibility that only sex cells with 9 chromosomes are viable, and the infrequent use of seeds as a means of propagation. However, in the early history of citrus culture, seedlings were commonly used in planting groves, and the disappearance of polyploid forms is apparently because they are of little or no value in horticul-

ture, as Frost points put. Longley emphasizes the possible value of the tetraploid *Fortunella hindsii* in hybridizing with closely related diploid forms to increase the chances of obtaining forms with unusual chromosome complexes.

Later, in 1925, Frost (*19*) reported on the discovery of certain "thick-leaved" apogamic seedlings of sweet orange (*Citrus sinensis*) and lemon (*C. limonia*) which proved to be tetraploids. He had observed such types to the extent of several percent of the total progeny in some cases in 12 horticultural varieties of citrus, representing 4 species, and in 2 botanical varieties, and he points out that they also may prove to be tetraploids.

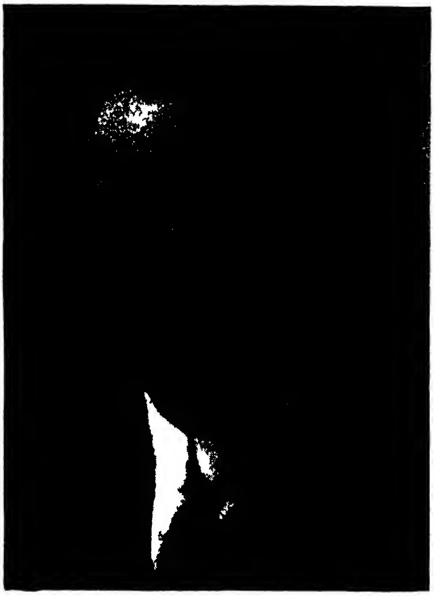

Figure 19.—Herbert J. Webber, pioneer worker in breeding citrus and other crops; United States Department of Agriculture, 1892–1907; Cornell University, 1907–12; California Agricultural Experiment Station, since 1913. He has carried on important work on rootstock variation as influenced by polyembryony.

As to the cause of these forms, Frost postulated the possibility of "islands" of tetraploid tissue in the parent trees, so that not all tetraploid seedlings represent distinct doubling of chromosome number. Against this view he found that the thick-leaved forms have not been found in mature trees by Shamel and his coworkers, and stated that this might be due to "the slower growth of tetraploid cells which might keep them from multiplying sufficiently to dominate the apical meristem, rather than to failure of tetraploidy to originate outside the nucellus." He further supported the hypothesis by citing the fact that in many cases a thick-leaved seedling has developed from a seed giving two or more nonhybrids, and in such cases the other apogamic seedlings from the same seed have almost always been normals.

In connection with these thick-leaved forms, Frost pointed out that they have not given promise of direct horticultural value, but they may be an aid in producing triploids or modified triploids by crossing with ordinary diploid forms, and that triploids would probably be practically seedless.

In 1926 Longley (*45*) reported his findings with reference to a triploid trigeneric hybrid, produced by Swingle and coworkers of the Department of Agriculture. This is a cross of the limequat (*Fortunella margarita* Swingle × *Citrus aurantifolia*) with *Fortunella hindsii*. Longley found 13 bivalent and a single univalent chromosome as the reduced number, and he found indications of only slight irregularity in chromosome distribution during meiosis in the triploid plant.

These findings led him to believe that triploids may be produced by appropriate crosses, and that in the case just cited or similar crosses there is a possibility of producing a seedless kumquat. More recently Longley [5] has found a second triploid, a sister hybrid of the first triploid found. Since most triploid plants are sterile, such crosses, it is hoped, may lead to developing seedless fruits. Longley later (April 1928) found an individual of *Triphasia trifolia* P. Wilson having 18 chromosomes.[5]

Polyembryony

In 1719 Leeuwenhoek noticed two embryos in orange seed, but it was not until 1878 that Strasburger (*65*) explained the true nature of the phenomenon of polyembryony in citrus as sporophytic budding from nucellar tissue. Frost (*19*) in 1925 found that in a minor portion of nucellar embryos—less than 1 percent—two hybrids were produced from one seed. Instances have been noted of three and even four—only two cases of the latter—apparently true hybrids produced from a single seed.[6] In one instance (lemon × trifoliate orange) out of 782 seeds, 16 produced 2 hybrids from 1 seed, with 1 producing 3 and 1 producing 4 hybrids, which is slightly more than 2 percent of "doubling."

Webber (*83*) (fig. 19), Frost (*20*), Toxopeus (*74*), and Torres (*73*) have shown that citrus types vary widely in the percentage of nucellar embryos produced (fig. 17). In a recent study made by Torres in the Philippine Islands, based on 50-seed samples, only the pummelo type did not exhibit polyembryony (table 2).

Table 2.—*Polyembryony in citrus in the Philippine Islands*

Citrus type	Average embryos per seed (range within type)	Embryos per seed (range—minimum and maximum)	Citrus type	Average embryos per seed (range within type)	Embryos per seed (range—minimum and maximum)
	Number	*Number*		*Number*	*Number*
Pummelo	1.0	---- ---	Sour orange	1.00 to 1.18±0.18	1 to 3
Grapefruit	1.16±0.23 to 2.86±0.89	1 to 6	Lime	1.0 to 1.20± .16	1 to 2
Sweet orange	1.32± .002 to 4.88±1.12	1 to 12	Tangelo	1.92± .45 to 2.32± .42	1 to 4
Citrus nobilis	1.02± .07 to 2.72± .44	1 to 6	Calamondin	5.32± .88	1 to 10
Lemon	1.30± .28 to 2.90± .88	1 to 6			

After summing up the evidence with reference to the effect of pollination on polyembryony, Frost (*20*) stated that it appears "very probable that citrus seeds do not develop without pollination, although seedless fruits sometimes develop without pollination even in varieties normally seedy." This would indicate that nucellar budding, which produces apogamic embryos, is at least very largely dependent on some growth stimulus due to the fertilized egg, as suggested by Strasburger (*66*) and Webber (*84*).

Frost (*20*) has shown that in interspecific crosses there is a negative correlation between the total number of seedlings and the percentage of hybrid seedlings, which shows the possible effect of competition among the embryos within the seed. During such developmental

[5] Unpublished work.
[6] Unpublished results of Swingle's crosses in 1909.

selection acting within the soma of the parent, the fertilized egg may be crowded out by the apogamic embryos, depending on the number of apogamic embryos that start and on the position and relative age and vigor of the two classes of embryos. Evidence as to selective elimination during germination was secured by noting the difference between the number of dissected embryos and the germination percentage in similar lots. During germination, survival may be determined by the "difference in size, vigor, position, morphological completeness, and susceptibility to infection." It was also noted that albinism causes the early death of many seedlings from some parents.

The variation in the number of nucellar embryos produced within a variety, and the possible effect of environmental conditions on such variation, led Traub (*76*) in 1936 to offer the hypothesis, based on preliminary experiments, that the number of nucellar embryos produced might be artificially varied by difference in food supply. If the preliminary results can be firmly established by experiments now in progress, an effective method for use in breeding work would be provided.

Swingle (*69*) postulated that citrus varieties propagated as clones are subject to senescence with age, and he cited the supposed disappearance or reduction in size of spines in well-established clones as one of the clearest indications of such senescence. He claimed that such clones might be at least partly rejuvenated, that is, become more spiny and vigorous, for instance, when seedlings from nucellar embryos were used as a method of establishing a new clone. This supposed nutritional effect of the embryo sac on the nucellar embryo developed within he named the "new-life" or "neophyosis" hypothesis.

However, there are no facts to prove that citrus clones are subject to senescence, and it is questionable whether the supposed rejuvenation is explainable as a permanent genetic factor change due to a nutritional effect or may be better explained by Frost's (*20*) theory of "islands" of mutating tissue in the nucellus.

Evaluation of Breeding Methods

Mass selection from open-pollinated seedlings was the method of citrus breeding followed by the early citrus growers It has yielded important results over long periods, but it is not now followed by any of the United States workers in this field. The search for bud variations and the use of hybridization are so much more promising that the method will be revived only for use in special cases.

The practical bearing of a rapid mutation rate in citrus has already been discussed in detailing the improvement of varieties. The question of the cause of such variations remains to be considered. It has been pointed out that Frost had postulated islands of tetraploid nucellar tissue as a possible explanation of the variation in apogamic seedlings, and the little that is known as to the cytological basis of citrus bud mutations has been ably discussed by Frost (*20*). The worker in this field does not have a background of abundant experimental data and must make use largely of the principles established by workers with more facile plant material such as maize, *Nicotiana*, etc., in developing useful theories.

On this basis Frost summarized the situation. Bud variations presumably originating in single cells by gene mutation or by differential mitosis are frequent in citrus. Frost says:

In the former case, at least, their somatic expression is doubtless favored by the presence of numerous heterozygous recessive genes. The production of recognizable bud variations, then, requires bud formation in an area of variant tissue, and may often be due to irregular tissue development in periclinal chimeras. The abundance of bud variation with some citrus forms apparently depends upon a permanent chimeral condition of the types in question.

The selection of bud mutations as a tool in citrus breeding has yielded some important results. Apogamic seedlings following interspecific crossing have given rise to the Davis grapefruit, the Silverhill satsuma orange, and the Oklawaha sour orange. In this group may be included the Everglade and Palmetto limes and Weshart and Trimble tangerines, although the supposed difference in these strains from the parental varieties has not warranted their continuance as distinct varieties. Evidence as to the behavior of the Lue orange indicates that this variety is apparently a nucellar seedling of the Valencia variety. A group of unnamed navel orange seedlings derived from seed of the Washington Navel pollinated with trifoliate orange pollen but showing no hybrid characters offer promise in securing new navel varieties adapted to Gulf coast conditions. In the same series, crosses made on the Thomson Navel gave only worthless fruits of the dry type, while a large percentage of the apogamic seedlings of the Washington Navel are vigorous growers and produce juicy fruits of more or less merit. If some of these prove to fruit satisfactorily under Florida and Gulf coast conditions, a navel variety may be found to meet the need in this section.

The work of Shamel and his coworkers in bud selection has preserved the original strains of commercial varieties and also yielded some superior new ones, as already detailed.

Chace, Church, and Denny (*8*, *9*) studied the inheritance of fruit composition in 18 mutant strains of Washington Navel orange and several mutant strains of Eureka and Lisbon lemons isolated by Shamel, Scott, Pomeroy, and Dyer (*63*, *64*). Chace and coworkers concluded that differences in the chemical composition of fruit exist between mutant strains, and that these are heritable. In Washington Navel strains some of these differences were closely connected with physical differences and others not. The differences generally found were in quantities of peel, oil, insoluble solids, and acids. Less variation was found in the specific gravity of the fruits and in the soluble solids and sugars of the juice. Strains of fruit with smooth skin were found to contain only small quantities of oil. In the Lisbon lemon mutants significant differences were found in specific gravity of fruit, proportion of rind, and percentage of acids; and in the Eureka lemon, in percentage of acids.

Haskins and Moore (*27*) observed premature flowering, albinism, fasciation, twisting, and peloric leaf formation in citrus seedlings grown from X-rayed seeds.

Selection within self-fertilized lines as a tool has little or no value in citrus breeding on account of polyembryony in most citrus types. The experience of Frost (*20*) at the Citrus Experiment Station has

shown that there is great loss of vigor and fertility with selfing. Toxopeus (*74*) and others have shown that the pummelo has no nucellar embryony and is usually self-pollinated. The progeny are usually quite uniform, and in such cases it is possible to develop more highly homozygous races by selection within self-fertilized lines.

Hybridization as a means toward the improvement of citrus varieties was undertaken by the Department in 1892 and has been continued ever since, and the progenies produced are being extensively tested in cooperation with the California, Florida, Texas, and Alabama experiment stations and many citrus growers (*70*, *71*, *84*, *86*). Some concrete results of definite value have been achieved as a result of this cooperation, as detailed under the improvement of citrus varieties above. Frost, in California, has carried on valuable work in this field since 1914, which has recently yielded promising citrus varieties. The work in Florida carried on by Camp and Jefferies, in Alabama by Yates, and in Texas by Yarnell and Wood was begun quite recently, and not enough time has elapsed to yield any definite results.

United States Department of Agriculture Breeding Results

Breeding work by the Department was initiated by Webber and Swingle and is carried out on the cooperative testing basis with the agricultural experiment stations and citrus growers in the subtropical fruit regions. The major part of the work is concerned with interspecific hybrids in which (1) the mandarin orange type is crossed with other citrus types with the object of securing high color of rind and flesh and also the "bouquet" of the tangerine in hybrid forms; (2) the lemon and lime are crossed with each other and with other citrus types; (3) bigeneric crosses of the trifoliate orange are made with species in other genera, primarily to increase the hardiness of the offspring; and (4) various crosses are made to explore the possibilities in other directions. The practical results from this work have been previously considered in the text and are summarized in table 7 of the appendix.

Mandarin Crossed With Other Citrus

Among the interspecific crosses that have given the most interesting results is the cross of the mandarin orange species on the grapefruit. In no case were hybrids produced when grapefruit pollen was transferred to the mandarin orange stigma, but the reverse operation has yielded abundant results.

The first crosses of this nature were made by Swingle in 1897 and by Webber in 1898. Webber and Swingle found wide variation in the F_1 progeny. Out of the first crosses two varieties were introduced, as already indicated, but in these the susceptibility to scab of the grapefruit parent was apparently dominant, and in addition the fruits were of such character that the keeping and shipping quality was unsatisfactory.

During the period 1908–12 Swingle, E. M. Savage, and F. W. Savage made a second series of crosses of a similar nature. The results were similar to those already stated, except that a number of the progeny were highly resistant to citrus scab and also possessed good shipping quality. An attempt was made to proceed a step farther through

selection from segregating seedlings in the F_2 generation, but on account of excessive nucellar embryony only one seminal seedling of merit was secured, which gave rise to a tangelo variety of promise, the San Jacinto. This was introduced in 1931.

A further attempt was made to secure desirable types by backcrossing the tangelo on the grapefruit, and in this case a fair number of seminal offspring were secured. In growth habit these resembled the pollen parent, the Sampson tangelo, but they were less vigorous. The fruit of two such backcrosses proved to be small, round, pink-fleshed, of low acidity and high sugar content, characters not present in either parent. One variety of the pink-fleshed backcross has been introduced as the Wekiwa.

Crosses made between the satsuma orange and the sweet orange have given rise to types somewhat similar to those secured by the tangerine-grapefruit cross with the flesh color and shape of the satsuma and the tight rind and size of the sweet orange (Ruby), but with high acidity and late maturity not found in either parent.

The third series of grapefruit-tangerine crosses were made by Traub, Robinson, and Savage, 1934–36, with the object of producing "seedless" tangelos. Marsh and its mutation, Thompson, and Davis, all "seedless" varieties, were used in place of Bowen, a seedy variety, which was chiefly utilized in previous crosses. These so-called "seedless" varieties are highly self-sterile and intersterile and produce few or no seeds even in mixed plantings.

Crosses between the tangerine and the sweet orange generally gave types similar to the latter but of small size.

Lemon-Lime Crosses

Among crosses between the lime and the lemon, the Perrine lemon, a promising variety, was found to be immune to citrus scab and lime withertip. It has already been mentioned and will be discussed more fully under disease resistance later.

Trifoliate Orange Crossed With Citrus and Fortunella Species

Citrus hybrids involving trifoliate orange (*Poncirus trifoliata*) as one parent have given rise to interesting results. The crosses were made by Swingle and Webber beginning in 1893 and at several times subsequently. In the first series 212 crosses were made and 13 hybrids (citranges, i. e., trifoliate × sweet orange) were secured. Most of these had the trifoliate orange as the seed parent, but in one case (Rusk citrange) the sweet orange produced the seed. There was wide variation in the characters of the hybrids. In most cases the leaves were of the trifoliate type, but unifoliate types were also secured. All were evergreen in habit; in fruit character there was also great variation in size, color, etc. In all cases the rind oil character was inherited from the trifoliate parent, and in most cases the juice character was intermediate. In none of the fruits was the juice character sufficiently like that of the sweet orange to give these fruits any prospect of commercial usefulness. Most of the progeny produced only nucellar embryos when an attempt was made to secure an F_2 generation by self-pollination, except in the case of the Sanford and Phelps citranges, which showed hybrids with segregation for leaf

characters. Seedlings of these segregating varieties were distributed for trial but thus far have produced nothing of special merit.

Hybrids were later secured by crossing the citrange and the kumquat. As a result the objectionable oil content of the fruit was reduced and an acid fruit type secured which has been called the citrangequat. One of the progeny, the Thomasville, shows high resistance to citrus canker, which was inherited apparently from the kumquat ancestor. The citrange crossed with calamondin has given an acid fruit type in which the disagreeable oil is eliminated. It has been called the Glen citrangedin. This type is relatively frost-resistant. Attempts made to secure the F_2 generation have been unsuccessful, since only nucellar embryos were secured.

Other Citrus Crosses

The lime crossed with the kumquat has given rise to small acid-fruited progeny which are immune to lime withertip and decidedly more frost-resistant than the true limes.

Various other crosses were made involving pummelo, sour orange, and other citrus species. The most interesting is the cross between the Eustis limequat, with a haploid chromosome number of 9, and the Hong Kong kumquat (*Fortunella hindsii*), with a haploid chromosome number of 18. This has given rise to a triploid hybrid, as reported by Longley, resembling the Hong Kong kumquat but larger and of greater vigor. It is of potential value in further crossing to secure seedless kumquat types, since many triploids are self-sterile and intersterile.

Inheritance in Citrus and Related Species

A number of hypotheses have been advanced to explain the wide variation in the progeny secured in the F_1 generation citrus crosses. Webber (*84*) in 1905 suggested that there must be some influence, either direct or indirect, of male parent on nucellar embryos, that the male element imparts the tendency to the segregation of characters that exist in the mother parent—characters that as a rule are probably of very mixed origin—but does not transmit any characters of the male parent. The Mendelian principles of unit factors, dominance, and segregation seemed inadequate to Swingle to account for his observations, and in 1913 he proposed the hypothesis of zygotaxis (*67*).

Swingle defined his hypothesis of zygotaxis as—

> the arrangement in syngamete (zygote) of the chromatin and other hereditary substances derived from the parental gametes and the persistence of this arrangement in the cells produced by the subdivision of the syngamete.

In further explanation of his hypothesis he states:

> It is assumed that the particular zygotactic arrangement taken up by the chromosomes of the parental gametes usually persists with little or no change throughout the life of the organism * * *. The fundamental idea underlying the term zygotaxis is that the architecture of the zygote with reference to its idioplastic particles, as well as its mechanisms for transmitting hereditary tendencies into expression, is determined to some extent at the moment of fusion of the two parental gametes and that this arrangement of parts is transmitted to the cells of the organism to which the zygote gives rise.

The hypothesis of zygotaxis was vigorously opposed by Hagedoorn and Hagedoorn (*25*) and by White (*89*). The former workers sug-

gested that variable F_1 progeny in citrus crosses apparently are due to habitual self-sterility and the sexual production of seeds. White points out that the F_1 variation in citrus hybrids, in the light of the data at hand, apparently results from differences in the gametic composition of the heterozygous parents.

Frost (*20*) sums up the evidence for and against the theory of zygotaxis and states that—

> enough is known of the production of new characters by new combinations of genes in crossing to warn us against setting any narrow limits to the probable results of recombinations in crosses between two highly heterozygous species. * * * It is concluded, from the available evidence, that citrus forms are in general extremely heterozygous. * * * This conception seems highly significant. * * * In the evolution of heterozygosis, polyembryony probably was an important factor.

Frost suggested that lethal and sublethal effects in selfing and crossing may be the result of homozygosis of inevitably unfavorable genes and may also be in part a result of incompatible recombinations. Heterosis, however, according to Frost, is probably more often secured in crossing.

Inheritance of Disease Resistance

The various citrus types and varieties show great variation in inheritance of resistance or susceptibility to various diseases. The summary given in table 3 is based largely on the text by Fawcett (*15*).

Winston, Bowman, and Bach (*90*) studied the resistance of citrus types and varieties to sour orange scab, *Sphaceloma fawcetti*, and found the following not susceptible: Kumquat; citron; Kansu orange (*Citrus junos* Tan.); Mexican, Woglum, and Tahiti limes; Royal and Triumph grapefruit; Cuban shaddock; Bergamot orange; most sweet oranges; and Cleopatra mandarin. The work of Peltier and Frederich (*52*) has shown that citrus scab cannot survive under California conditions, indicating that susceptibility under certain conditions may not be apparent.

Fulton (*22*) made a study of the susceptibility of citrus types and varieties to Key lime withertip or anthracnose (*Gloeosporium limetticolum*). He found that the West Indian (Key) lime and the Dominican (thornless) lime are highly susceptible. Other lime varieties have not given undoubted evidence of susceptibility. Hybrid West Indian limes, sweet orange, grapefruit, lemon, *Citrus nobilis*, and others have proved immune. Since only two types are highly susceptible, it is suggested that other closely related varieties might be substituted in culture. It is interesting to note that susceptibility seems not to be a dominant factor in F_1 hybrids.

Peltier and Frederich (*51*) made extensive studies of the susceptibility of *Citrus* and related genera to citrus canker (*Pseudomonas citri*) under greenhouse and Gulf coast conditions. Lee (*41, 42*) made similar studies in the Orient. Although there is no immediate need for varieties and stocks resistant to citrus canker, since the epidemic in the upper Gulf coast and in Florida has been practically eradicated since 1925, it is of advantage to select resistant types where possible as an insurance in case the disease should be inadvertently reintroduced. Grouped in order of susceptibility, varieties of grapefruit and pummelo (shaddock) proved extremely susceptible (except two pummelo varieties, Hirado and Siam, and the Triumph grape-

TABLE 3.—*Relative susceptibility of citrus species and varieties and related species to principal diseases*

[++ indicates high, + medium, and ± slight susceptibility, − indicates high degree of immunity or practically complete immunity]

Species or variety	Mal di gomma (foot rot)	Brown rot gummosis [1]	Psorosis	Bark rot of Orient	Decorticosis	Melanose	Sour orange scab	Sweet orange scab	Australian citrus scab	Canker	Blast	Citrus anthracnose [2]	Key lime anthracnose	Black spot (*Phoma*)	Phyllosticta leaf drop of Orient	Leprosis (nail-head rust)	Mal secco
Sweet orange (*Citrus sinensis*)	++	++	++	−	−	++	−	++	±	+	++	+	−	++		++	−
Sour orange (*C. aurantium*)	−	−	±		−	++	++	−	++	+	+	+				−	++
Lemon (*C. limonia*)	++	++			++	+	++		++	+	+	+		+		±	++
Rough lemon	+	+	−			+	++									±	
Lime (*C. aurantifolia*):																	
Key lime		+				+	−			++		−	++			+	+
Sweet lime		+					±	+		+			−				+
Citron (*C. medica*)	++	+			−	+	−			±		+				±	++
Grapefruit (*C. grandis*)	+	+	+	−	−	++	++		−	++	+	+		+	+	−	+
Pummelo (*C. grandis*)	+	++	+	−	−	++	+			++	+	+		+		−	+
King orange (*C. nobilis*)							+			+				+			
Tangerine (*C. nobilis* var. *deliciosa*)	+	+	++	++	−	+	+	+	+	±	±	+		+		±	−
Satsuma (*C. nobilis* var. *unshiu*)	+	±		++	−	+	+		+	±	±	+		+	++	−	−
Calamondin (*C. mitis*)		−		±			++			±							
Kumquat (*Fortunella* spp.)		−					±			±							
Trifoliate orange (*Poncirus trifoliata*)							+			++							+
Eremocitrus glauca (Lindl.) Swingle							−			−							
Severinia burifolia (Poir.) Ten.		−					−			−							
Chaetospermum glutinosa (Blanco) Swingle										++							
Citropsis spp.										−							

[1] Some pummelo varieties resist brown rot gummosis; others are very susceptible.
[2] Anthracnose of citrus other than Key lime.

fruit). Lemon varieties and the trifoliate orange (*Poncirus trifoliata*) are only slightly less susceptible than grapefruit. Classed as moderately susceptible are the sweet oranges, sour oranges, citrons, and limes, except that the Tahiti lime is much less susceptible than the Mexican lime. The mandarin group (*Citrus nobilis* varieties) as a whole is only slightly attacked, as is also the calamondin. The outstanding resistant members of the edible citrus fruit group proved to be the kumquats (*Fortunella* spp.), except the susceptible Hong Kong kumquat (*F. hindsii*), resistance in kumquats amounting to practical immunity under field conditions.

The extensive citrus canker tests made by Peltier and Frederich (*51*) afforded opportunities for testing the numerous hybrids developed by the Department, these hybrids involving reciprocal crosses between numerous species and varieties ranging in their reaction to canker infection from extremely susceptible to very resistant. The results of these tests may be briefly summarized as follows. All the trifoliate orange first crosses proved quite susceptible to canker, like the parent, *Poncirus trifoliata*. In the second cross, that is, citranges crossed with other parents, those hybrids with the mandarin orange or the kumquat as one parent proved decidedly resistant; in fact, the citrangequat (Thomasville variety) proved practically immune, fully as much so as the kumquat. Likewise the limequat and the orangequat can be regarded as similar to the satsuma in resistance. The calamondin, while somewhat resistant itself, does not carry this resistance into the hybrid, with one exception, the citrangedin (citrange × calamondin). Most of the grapefruit hybrids have proved quite susceptible, although certain of the tangerine and satsuma crosses with grapefruit (tangelos) show enough canker resistance to place them beside the mandarin oranges in their resistance to canker. Peltier and Frederich conclude: "In the search for promising canker-resistant plants the results of over 4 years' investigations seem to point to the fact that our best plants will come from the hybrids."

Gummosis, a disease caused by *Phytophthora citrophthora*, has been studied by Klotz and Fawcett (*37*), who tested 78 species and varieties for resistance. The sour oranges proved very resistant, while the lemons were most susceptible. Klotz (*36*) has shown that the resistance apparently is due to some cellular product of the host that has an inhibiting action on the fungoid enzymes.

Toxopeus (*75*) reported that the factor or factors for resistance to foot rot (*Phytophthora parasitica*) might possibly be recessive, and in that case he suggests that selection for individuals resistant to this disease be made in the second generation (F_2) after crossing

Inheritance of Capacity to Produce Vitamins

Preliminary tests have been made indicating how capacity to produce vitamins is transmitted in citrus hybrids. The only published report (*71*) has to do with tests made in 1928 with the Sampson and Thornton tangelos, comparing the vitamin B content of these hybrids with that of the parental varieties, grapefuit and tangerine. These tests, made by the Bureau of Chemistry and Soils of the Department, were summarized as follows:

Both charts are in agreement in showing tangerine juice to be a better source of vitamin B than the juice of the other fruits fed, and also that tangelo juice is approximately equal in vitamin B potency to grapefruit juice. Therefore, with respect to vitamin B production the tangelo has inherited the characteristics of the grapefruit (*71, footnote, p. 3*).

With respect to vitamin C, which is of still more importance in the citrus fruits, tests are in progress and some indications as to inheritance have already been secured. These preliminary tests (*13*) were made during the 1935–36 season by Esther P. Daniel, Bureau of Home Economics, in cooperation with Traub and Robinson, Bureau of Plant Industry, of the Department. In these tests the ascorbic acid content of fruit samples at maturity was determined by the titration method. The figures below indicate milligrams of ascorbic acid per cubuc centimeter of juice:

The Thornton and Orlando tangelos (range 0.33 to 0.35) gave results approximating those of the Bowen grapefruit parent (average 0.35); the Sampson, Minneola, and Seminole (range 0.18 to 0.28) proved more like the Dancy tangerine parent (average 0.24). One variety that was grouped with the tangelos, the Umatilla, but that in fact is a hybrid between satsuma and Ruby oranges, gave a much higher content of ascorbic acid (0.40) than the true tangelos. The Clement tangelo, which has the Clementine as the pollen parent, had the highest content (0.64). The Clementine is reputed to be a natural hybrid between the sour orange and the tangerine and has a higher content of ascorbic acid (0.37) than the Dancy (0.24).

The Perrine lemon—a hybrid of lemon and lime—appears to inherit from the lemon parent rather than from the lime, having an ascorbic acid content of 0.40 as compared with 0.22 in the lime.

The limequat (Lakeland) ranks low (0.17), like the lime parent. It is interesting to note that the sweet lime (often called sweet lemon) has a fairly high ascorbic acid content (0.33), despite its almost complete lack of citric acid. Apparently there is no positive correlation between citric and ascorbic acid content.

Results at State Stations

California

The hybridization work at the Citrus Experiment Station at Riverside was begun by Frost (*17*) in 1914, and since that date pollinations were made mainly in 1915, 1916, 1928, 1929, and 1931. More work of this nature is planned for the next 2 or 3 years. The work consists of selfing and crossing and the study of genetic variation in nucellar seedlings.

In general the work is confined to crosses between species and within the mandarin orange group, *Citrus nobilis*. In all cases selfing of the parents is carried along as far as practicable with the work of crossing. In all, six varieties of sweet orange, three of grapefruit, and four of lemon have been used in crossing. Within the mandarin group four varieties were used in crosses. The chief results so far have been secured by selection within the first generation (F_1), but promising F_1 hybrids have been selfed, and crosses have been made between promising hybrids and standard varieties.

The F_1 hybrid combinations represented by at least one individual include the following: Lemon and mandarin (tangemon), mandarin and mandarin (of distinct botanical varieties), orange and mandarin (tangor), grapefruit and mandarin (tangelo), grapefruit and orange (orangelo), lemon and orange (oramon), and grapefruit and lemon (lemelo). The most promising hybrids not yet introduced seem to

be the following: One each from King mandarin × Dancy tangerine (fruit of very good size, fair shape, and very good flavor); from Mediterranean Sweet orange × Dancy tangerine (very good fruit color and flavor, extra early); and from satsuma (Owari) × Lisbon lemon (fruit rough, very juicy, seedless, high in acid, excellent in aroma).

The most promising results have been secured by crossing within the mandarin group. Three varieties already mentioned have been introduced, and at least two or three more are under consideration as candidates for introduction. The earliest work at the Citrus Experiment Station led to the use of the King mandarin as the main seed parent in these crosses.

During the last few years certain hybrids from crosses of lemons with grapefruit and of "hedge bergamot" with grapefruit have been studied as possible stock types for lemons. On the basis of tree characters, seed production, and resistance to inoculated phytophthora gummosis, several hybrids have been selected for further trial, and a preliminary study of seedlings has been made. At present one hybrid from Imperial grapefruit × hedge bergamot and one from Eureka lemon × Imperial grapefruit seem most promising, although it is not certain whether they have enough nucellar embryony to produce adequately uniform seedlings for rootstocks.

A general survey including 3,800 trees is under way in a search for genetic differences from the seed parent. Tetraploids are listed and studied, and a special study is being made of a few other progenies showing unquestionably variant characters (dry fruit from one parent tree, nonnavel fruit and pollen production from two navel parent trees without pollen, late-ripening fruit from one parent tree). A study of possible genetic differences in fruit shape (satsuma) and pulp color (blood orange) among progeny of the same seed-parent tree has also been undertaken.

The related specialized studies carried on by Frost include:

(1) *Polyembryony.*—Counts of total embryos and counts of generative and nucellar seedlings have been made for horticultural varieties, tetraploid and diploid nucellar progeny, and F_1 hybrids. Among about 1,200 hybrids, 10 cases of duplicate hybrids (two identical hybrids from one seed) have been found, obviously the result of embryonic fission. Nucellar embryos seem to be somewhat less abundant with tetraploids than with corresponding diploids.

(2) *Triploidy and tetraploidy.*—About 2 percent of about 3,800 nucellar seedlings were tetraploid and have been especially studied. These are of no horticultural value. A few hybrids have recently been produced by crossing a tetraploid with diploids as pollen parents; the reverse combination failed to produce seed. About 1½ percent of about 1,200 hybrids have been proved to be triploid, none tetraploid; several times as many are suggestive of triploidy, but their chromosome constitution has not been determined.

(3) *Chromosome behavior.*—Preliminary studies have been made on chromosome conjugation and segregation in diploids, triploids, and tetraploids, and on irregularities at the microsporad stage.

(4) *Clonal senescence.*—Studies are in progress on various juvenile characters of young seedlings and clones, especially thorniness, scarcity of flowers, and general vigor of growth, and on their decline with increasing age from seed and increasing length of shoot growth.

(5) *Chimeras and bud variation.*—Studies of tree and fruit characters have been made on forms that seem to be chimeral, in the general variety collection of citrus.

Florida

The citrus hybridization work by Camp and Jefferies at the Florida State Citrus Experiment Station, Lake Alfred, with acid citrus fruits was begun in 1924. Numerous crosses have been made, including 18 different combinations, with the following as parents: Calamondin; Rangpur lime; Meyer, Genoa, and Villa Franca lemons; Jamaica and Key limes; and the limequat. The F_1 progency have reached the fruiting stage and are under test.

The work carried on in cooperation with the Department is concerned with bud selection and with the testing of the citrus varieties originated by the Department.

The citrus progeny testing collection, begun in 1921, contains 52 strains of oranges, tangelos, grapefruit, and tangerines selected from record trees, and these have been intensively studied. From the superior strains budwood has been distributed in quantity to nurserymen. Selections from Thompson and Marsh grapefruit and Valencia, Hamlin, Parson Brown, Temple, and Pineapple oranges are in greatest demand.

The Department hybrids have been tested out over a long period. According to the latest report, the utilization of Rusk and Morton citranges as rootstocks for the satsuma orange is promising.

Alabama

The citrus work of the Alabama Agricultural Experiment Station, begun in 1933 in cooperation with the Department, is concerned with the testing out of over 50 strains of the satsuma orange, both early- and late-maturing, and with the selection in the F_2 generation of citrange, particularly for high quality fruit and cold resistance. The experiments have not been carried on for a sufficient period to yield concrete results, although several of the recently introduced satsuma orange strains appear promising for hardiness, early bearing, and fruit quality.

Texas

The citrus breeding work begun by Yarnell and Wood at the Texas Agricultural Experiment Station in 1934 comprises a study of the adaptability of citrus varieties and citrus relatives, both for fruit and rootstock purposes; mass selection of open-pollinated citrange seedlings, primarily for cold resistance; crossing and selfing in sweet orange, mandarin orange, grapefruit, and acid citrus fruits. In all cases of crossing and selfing some cytological studies of root tips, buds, and young fruits are also carried along.

The following rootstock plants introduced primarily by the Department are under test: (1) *Balsamocitrus paniculata* Swingle; (2) citradia; (3) *Citrus aurantifolia*—Key, Mexican, Rangpur, Tahiti; (4) *C. aurantium*—African, Bittersweet, Brazilian, Paraguay, Roubidoux, Rough Seville, standard Sour; (5) *C. bergamia* Risso; (6) *C. ichangensis;* (7) *C grandis*—Triumph; (8) *C. limetta* Risso—sweet lime; (9) *C. limonia*—Keller, Meyer, Perrine, Ponderosa, Rickart, Rough; (10) *C. maxima* Marr.—Chinese pummelo, Cuban and Pink shaddocks; (11) *C. medica*—Diamante, Etrog, Indian, Italian; (12) *C. mitis*—calamondin; (13) *C. nobilis*—Cleopatra; (14) *C. sinensis*—Oroville,

Weldon, Raymondville; (15) citrange; (16) citrangedin—Glen; (17) citrangequat—Thomasville; (18) citrumelo (citrange × pummelo); (19) limequat—Lakeland, Tavares; (20) Suen Kat orange; (21) tangelo—Altoona, Clement, Lake, Minneola, Sampson, Seminole, Thornton, Umatilla, Wekiwa, Yalaha.

The following crosses have been made: (1) Sweet orange—Ruby × Hamlin, Valencia × Hamlin, Ruby × Meyer lemon and reciprocal, Parson Brown × Meyer lemon and reciprocal, Parson Brown × Ponderosa lemon, Pineapple × Pink Marsh grapefruit, Valencia × citron; (2) mandarin orange and hybrids—Meyer lemon × Clementine tangerine, Meyer lemon × Owari satsuma, Owari × Hamlin orange, Owari × Pink Marsh grapefruit, Thornton × Clementine, Thornton × Pink Marsh; (3) grapefruit—Meyer lemon × Pink Marsh, Pineapple orange × Pink Marsh, satsuma orange × Pink Marsh, Thornton tangelo × Pink Marsh; (4) acid citrus fruits—Meyer lemon × Pink Marsh grapefruit, Meyer lemon × Mexican lime, Meyer lemon × Clementine tangerine, Meyer lemon × Eureka lemon, Meyer lemon × citron, Meyer lemon × Ruby orange, Meyer lemon × satsuma orange, Meyer lemon selfed, Parson Brown orange × Meyer lemon, Parson Brown orange × Ponderosa lemon.

The citrus varieties originated by the Department, and also introductions from abroad, have been tested out on a cooperative basis since 1930. The most promising variety in the testing collection at the Texas substation at Weslaco up to the present time is the Texas Navel, to which reference has already been made. In cooperation with the Department more than 50 strains of the satsuma orange, both early and late maturing, are under test at Texas substations at Angleton and Winter Haven, and attempts to select desirable individuals of high quality and resistant to low temperatures in second generation citrange progeny are under way at College Station.

Hawaii

The Hawaii Agricultural Experiment Station (*28*) reports that rootstock and variety tests are in progress to determine the suitability of various combinations of scion and rootstock to different sites and soils. Many recent introductions of promise are being tested in comparison with the older standard varieties.

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APPENDIX

UNITED STATES SUBTROPICAL AND TROPICAL FRUIT-BREEDING STATIONS AND EARLY AND PRESENT WORKERS

[An asterisk (*) designates workers all or part of whose salaries were or are paid from Federal funds]

(1) United States Department of Agriculture, Washington, D. C.:
Early workers—*H. J. Webber, *W. T. Swingle, *Eugene May, *Frank W. Savage, *R. E. Caryl, *L. B. Scott.
Present workers—*Hamilton P. Traub, senior horticulturist; *T. Ralph Robinson, senior physiologist; *Edward M. Savage, assistant plant breeder; *A. D. Shamel, principal physiologist; *C. S. Pomeroy, associate pomologist; *A. E. Longley, associate botanist.

(2) Alabama Agricultural Experiment Station of the Alabama Polytechnic Institute, Gulf Coast Substation, Fairhope:
Present workers—*Harold F. Yates, acting superintendent.

(3) Arizona College of Agriculture and the Agricultural Experiment Station, Tucson:
Present workers—W. E. Bryan, head of Department of Plant Breeding (date breeding).

(4) California College of Agriculture and the Agricultural Experiment Station of the University of California:
Early workers—C. S. Milliken, C. L. Dyer, F. N. Harmon.
Present workers—H. J. Webber, emeritus professor of subtropical horticulture, Riverside; Ira J. Condit, associate professor of subtropical horticulture, Riverside; L. D. Batchelor, director of Citrus Experiment Station, Riverside; Robert W. Hodgson, head of Division of Subtropical Horticulture, Los Angeles; R. E. Caryl, associate in orchard management, Riverside; H. B. Frost, associate plant breeder, Riverside.

(5) College of Agriculture and Agricultural Experiment Station of the University of Florida:
Early workers—H. H. Hume, John Belling.
Present workers—H. S. Wolfe, horticulturist in charge, Subtropical Experiment Station, Homestead; A. F. Camp, horticulturist in charge, Citrus Experiment Station, Lake Alfred; J. H. Jefferies, superintendent, Citrus Experiment Station, Lake Alfred.

(6) Glen St. Mary Nurseries Co., Glen St. Mary, Fla.:
Early workers—G. L. Taber (trifoliate rootstock investigations), H. Harold Hume (persimmon investigations).

(7) University of Hawaii and the Hawaii Agricultural Experiment Station:
Early workers—*J. E. Higgins, *V. S. Holt, *J. M. Westgate.
Present workers—*J. H. Beaumont, principal horticulturist; *W. T. Pope, senior horticulturist; *R. H. Moltzan, principal scientific aide; *J. C. Thompson, principal scientific aide; *W. B. Storey, junior biological aide.

(8) Louisiana State University and Agricultural and Mechanical College and the Agricultural Experiment Station:
Present worker—J. C. Miller, horticulturist in charge of research.
(9) Puerto Rico Agricultural Experiment Station, Rio Piedras, Puerto Rico:
Early worker—O. W. Barrett.
Present worker—Julio S. Simons, agronomist for plant introduction and propagation.
(10) Federal Experiment Station, Mayaguez, Puerto Rico:
Early workers—*O. W. Barrett, *Holger Johansen, *T. B. McClelland.
Present worker—*C. L. Horne, associate horticulturist.
(11) Panama Canal Zone Experiment Gardens, Summit:
Present workers—*J. E. Higgins, consultant in plant introduction and utilization; *Walter R. Lindsay, acting director.
(12) Commonwealth of the Philippines, Department of Agriculture and Commerce (citrus, avocado, pineapple, and papaya breeding):
(a) Bureau of Plant Industry, Manila:
Early workers—C. F. Baker, T. P. Reyes, P. J. Wester.
Present workers—J. P. Torres, J. de Leon, F. Galang, F. K. Morada.
(b) College of Agriculture, University of the Philippines, Department of Agronomy, Laguna:
Present workers—N. B. Mendiola, plant breeder and geneticist; J. M. Capinpin, plant breeder and cytologist; T. Mercado, assistant plant breeder.
(13) Texas Agricultural Experiment Station:
Present workers—S. H. Yarnell, chief, Division of Horticulture, College Station; J. F. Wood, horticulturist, Weslaco; H. M. Reed, horticulturist, Angleton.

Subtropical and Tropical Fruit-Breeding Stations in Foreign Countries and Workers and Present Work

Europe and North Africa

Spain:
(1) Estacion Naranjera de Levante, Burjasot, Valencia (citrus breeding):
Present worker—Manuel Herrero.
Italy:
(2) Regia Stazione Sperimentale de Olivicoltura ed Oleificio, Pescara (olive breeding):
Present worker—Julio Savastano.
(3) Regia Stazione Sperimentale di Frutticoltura e de Agrumicoltura, Arcieale Catania, Sicily (breeding for resistance to mal secco in lemons).
French Morocco:
(4) Experimentation Fruitière et Maraichère, Rabat (citrus breeding):
Present workers—F. Lacarello, Director; Ch. Miedzyrzecki, geneticist.
Greece:
(5) Hellenic Kingdom Superior School of Agriculture, Laboratory of Horticulture, Athens (olive and fig variety studies):
Present worker—P. Th. Anagnostopolous.

Asia and Malaya

Palestine:
(6) Jewish Agency, Agricultural Experiment Station, Rehoboth (citrus breeding):
Early worker—J. D. Oppenheim.
Present worker—Ch. Oppenheimer.
(7) Agricultural School, Mikweh-Israel (collection of Jaffa orange bud mutations):
Present worker—S. Yedidja.
India:
(8) Poona, Bombay Presidency; Horticultural Section (1) Ganeshkhind Fruit Experiment Station, Kirkee; (2) Modibag (Garden), College of Agriculture, Poona. (Improvement of citrus, mango, papaya, pineapple, guava, pomegranate, fig, banana, jujube, annona.)
Early workers—W. Burns, S. H. Prayag, L. B. Kulkarni, H. P. Paranjpe.
Present workers—G. S. Cheema, horticulturist and professor of horticulture; P. G. Dani, assistant; S. R. Gandhi, assistant; S. S. Bhat, assistant; B. Nazareth, assistant.

(9) Department of Agriculture, Bihar (mango and papaya breeding):
Present workers—R. Zarbakht-Kahn, horticulturist; R. Shah, assistant; S. Prashad, assistant.
(10) Royal Agricultural and Horticultural Society of India, Alipur, Calcutta (variety studies of tropical fruits):
Present worker—Sydney Percy Lancaster.
(11) Government Gardens, Saharanpur, United Provinces (lime, mango, and loquat improvement):
R. D. Fordham, deputy director.
Straits Settlements and Federated Malay States:
(12) Department of Agriculture, Kuala Lampur (pineapple breeding):
Present worker—W. D. P. Olds, director of agriculture.
Siam:
(13) Department of Agriculture and Fisheries, Bangkok (variety studies of tropical fruits):
Present worker—Luang Suwan, director general.
China:
(14) College of Agriculture, Lingnan University, Canton; Department of Horticulture (variety studies of citrus, avocado, mango, papaya, pineapple, banana, lychee, diospyros, annona, artocarpus, Chinese olive (*Canaria*), etc.):
Present workers—G. Weidman Groff, professor of horticulture; Pui-man Lei, Iu-nin Shiu, A. N Benemerito.
Japan:
(15) Imperial Horticultural Experiment Station, Okitsu (fig, loquat, and citrus breeding):
Present worker—T. Tanikawa, acting director.
(16) Chiba Horticultural College, near Tokyo (loquat variety studies):
Present worker—Taiji Miki, professor of pomology.
(17) Shizuoka Agricultural Experiment Station (bud mutations of satsuma orange):
Present worker—Kimijiro Noro, pomologist.
(18) Taihoku Imperial University, Formosa (citrus breeding):
Present worker—Tyozaburo Tanaka, professor of citriculture.
(19) Agricultural Experiment Station, Shirin, Taihoku, Taiwau (subtropical fruit crops breeding):
Present worker—Y. Sakurai, pomologist.
Netherland East Indies:
(20) Buitenzorg Botanical Gardens (improvement of citrus and other tropical fruits):
Present workers—G. J. A. Lirra, horticultural adviser; H. J. Toxopeus, geneticist.

South and Central Africa

Union of South Africa:
(21) Division of Plant Industry, Union of South Africa; Subtropical Horticultural Research Station, Nelspruit, Eastern Transvaal (papaya and pineapple breeding):
Present worker—J. D. J. Hofmeyr, research horticulturist.
(22) Department of Pomology, University of Stellenbosch (fig and olive variety trials):
Present worker—O. S. H. Reinecke, head of department of pomology.
Southern Rhodesia:
(23) Citrus Experimental Station, Mazoe (citrus variety trials):
Present worker—L. A. Lee, horticulturist.
Zanzibar, East Africa:
(24) Department of Agriculture (variety trials—citrus, banana, pineapple, mango, papaya, lychee, and rambutan):
Present worker—A. J. Findley, director.
Nigeria:
(25) Agricultural Department, Ibadan (breeding of pineapple, and variety trials with citrus, mango, avocado, and papaya):
Present worker—E. H. G. Smith, agricultural botanist.

Australia and New Zealand

Victoria:
(26) Department of Agriculture, Division of Horticulture, Melbourne (bud selection in citrus):
Present worker—J. M. Ward, superintendent of horticulture.
New South Wales:
(27) Grafton Experiment Farm and the Hawkesbury Agricultural College (citrus breeding).
Queensland:
(28) Department of Agriculture and Stock, Brisbane (improvement of citrus, avocado, mango, papaya, pineapple, date, olive, granadilla, persimmon, fig, loquat, and guava):
Present worker—(Appointment of research staff in fruit crops now under consideration).
(29) Queensland Acclimatisation Society, Brisbane (introduction of tropical and subtropical fruits):
Present worker—R. Allsopp, overseer.
New Zealand:
(30) Department of Agriculture, Horticulture Division, Wellington (citrus, avocado, and olive variety trials):
Present worker—J. A. Campbell, director, Horticulture Division.
(31) Department of Scientific and Industrial Research, Plant Research Bureau, Mount Albert, Auckland (subtropical fruit variety trials):
Present worker—Dr. Allen.

Mexico, Central America, and the Antilles

Mexico:
(32) Estacion Experimental:
(a) Acapulco, Guerrero (mango, lime, pineapple, and avocado).
(b) Oaxaca, Oaxaca (mango, lime, avocado).
(c) Jalapa, Veracruz (papaya, mango, pineapple).
(d) Colima, Colima (lime).
(e) Leon, Guanajuato (avocado).
(f) Queretaro, Queretaro (avocado).
(g) Coalan del Rio, Morelos (papaya).
(h) Hecelchakan, Campeche (avocado).
Honduras:
(33) Lancetilla Experiment Station (United Fruit Co.), Tela (Extensive tropical fruit variety trials):
Present worker—Wilson Popenoe, agricultural director.
British Honduras:
(34) The Agricultural Office, Belize (introduction and testing of citrus varieties):
Present worker—H. P. Smart, agricultural officer.
Costa Rica:
(35) Alan Kelso, Aparto. 246, Punta Arenas. (Private work; tropical fruit crop introduction and improvement.)
Cuba:
(36) Agricultural Experiment Station, Santiago de las Vegas (variety tests and selections of citrus, avocado, mango, banana, and pineapple):
Early workers—M. Fortun, J. Ajete.
(37) Atkins Institution of the Arnold Arboretum (Harvard University), Cienfuegos (breeding of citrus and other tropical fruits):
Present worker—H. C. Gray, director.
Jamaica:
(38) Department of Agriculture, Hope, Kingston (papaya and banana breeding):
Present worker—L. N. H. Larter, Government botanist.
Trinidad, British West Indies:
(39) The Imperial College of Tropical Agriculture (banana and other tropical fruits breeding):
Present worker—E. E. Cheeseman, professor of botany.

South America

Chile:
(40) Salvador Izquierdo, Monedo 778, Santiago.
(Private work confined mostly to introduction of new varieties of subtropical fruits.)

Brazil:

(41) Instituto Agronomico do Estada de São Paulo, Genetics Department (citrus and banana breeding):

Present worker—C. A. Krug, head of department.

Argentina:

(42) Estacion Experimental de Concordia, Ministerio de Agricultura de la Nacion Argentina (citrus breeding):

Present worker—Ruben Bence Pieres, ing. agr. and director of the station.

TABLE 4.—*Chromosome numbers of Citrus species and varieties and related species (family Rutaceae) as far as determined up to 1936*

[See literature citations *18, 19, 23, 24, 33, 44, 45, 47, 49, 72*]

Species or variety	Chromosome number (*n*)	Authority and year determined	Remarks
Aeglopsis chevalieri	9	Longley, 1925	
Triphasia trifolia	9	do	
Triphasia trifolia var. *bivalens*	18	Longley, 1937	Determined in 1928.
Severinia buxifolia	9	Longley, 1925	Do.
Microcitrus australis	9	Longley, 1937	
Citropsis schweinfurthii	9	Longley, 1925	
Poncirus trifoliata	9	do	
Fortunella crassifolia	9	do	
F. margarita	9	do	
F. japonica	9	do	
F. hindsii	18	do	
Citrus medica	9	do	
C. limonia	9	Frost, 1925 Longley, 1925	
C. limonia var. *bivalens*	18	Frost, 1925	
C. aurantifolia	9	Longley, 1925	
C. grandis	9	do. Frost, 1925	
C. aurantium			Undetermined.
C. sinensis	9	Frost, 1925; Longley, 1925; Oppenheimer and Fraenkel, 1929.	
C. sinensis var. *bivalens*	18	Frost, 1925	
C. nobilis	9	Longley, 1925	
C. nobilis var. *deliciosa*	9		Quoted by Oppenheimer (*49*) without citation of author.
C. nobilis var. *unshiu*	9	Nakamura, 1929	
C. mitis	9	Longley, 1925	
C. ichangensis			Undetermined.

TABLE 5.—*Citrus species and varieties introduced by the United States Department of Agriculture*

Species	Common or varietal name	Native habitat	Source of introduction	Where now available	Remarks
Citrus grandis	Shaddock	Southeastern Asia	Original habitat; also Australia, West Indies, South Africa.	Orlando, Eustis, Coconut Grove, and Lake Alfred, Fla., Riverside, Calif., Weslaco, Tex.	Cuban shaddock is being tested for possible use as rootstock; Arajan (pink,) Alamoen
Do	Pummelo	Southeastern Asia, Malaysia.	Siam, China, India, Philippines, Hawaii.	Eustis, Fla	The following varieties are being tested for utilization of fruit and resistance to saline soil solution: Kao Pan, Kao Phuang, Thong Dee, Nakorn, Victoria, Siam, Pandan Wangi, Better Pummelo, Wong Yau, Banda, Indian Red.
Do	Grapefruit	do	South Africa	do	Cecily grapefruit, reputed to be a seedless mutation, being tested for difference, if any, from standard seedless varieties.
C. aurantium	Sour, Bigarade, or Seville orange.	China, southeastern Asia.	Original habitat; also Spain, North Africa, West Indies, Australia.	Orlando, Eustis, Coconut Grove, and Lake Alfred, Fla., Riverside, Calif.	For testing as semihardy and disease-resistant stocks for use in hybridization, for utilization as marmalade fruits.
	Chinotti		Southern France	do	A preserving fruit; also useful as a potted dwarf plant.
	Bergametto (bergamot orange).		Sicily	do	Used in preparing flavoring extracts and perfumes.
C. sinensis (sweet orange).	Washington Navel or Bahia Navel.	China, southeastern Asia.	Brazil	do	The original introduction which served as a basis for developing the orange industry of California. Other varieties, as the Thomson Navel, have sprung from this variety. Not adapted to Florida culture.
	Texas Navel	do	do	Weslaco, Tex., Riverside, Calif.	Several navel types (seedless) introduced by Dorsett, Shamel, and Popenoe; one of which is being propagated in southern Texas as the Texas Navel for testing and breeding.
	Algerian	do	Algeria	Orlando and Eustis, Fla	Reputed to be productive and of good quality; being tested, not yet fruiting.
	Matidja	do	do	do	Do.
	Zatina	do	do	do	Do.
	Chamoudi (Shamooti)	do	Palestine	Orlando, Eustis, and Coconut Grove, Fla., Riverside, Calif., Weslaco, Tex.	A large seedless orange, famous as the "Jaffa" orange in European markets; for testing its adaptability and for use in hybridization.
	Capuchin	do	Chile	Orlando, Eustis, and Oneco, Fla.	Small, hardy orange; useful as potted ornamental and in breeding.
	Telde	do	Canary Islands	Orlando and Eustis, Fla	Small-fruited sweet orange; reputed of high quality; for testing and breeding.
	Lau Chang, Hang Chang.	do	China	do	Sweet orange reputed to be of high quality; for testing and breeding; not yet fruiting.
	Harvard	do	Cuba	Orlando, Coconut Grove, and Eustis, Fla.	An early-maturing orange, reputed to be of hybrid origin; for testing.

	Tankan	do	Formosa	do	A small disease-resistant, late-maturing orange of high color Used for testing and breeding
	Rico	do	Puerto Rico	Orlando and Eustis Fla Riverside Calif, Weslaco Tex	Rico, nos 1 to 6 Six selections made from seedling oranges for seedlessness and quality not yet fruiting
	Selecta	do	Brazil	do	Parent variety of the Washington Navel
	Byfield seedless	do	Australia	Orlando Fla	Reputed to be a midseason orange, seedless, of good quality Not yet fruiting
C nobilis var *deliciosa* (mandarin group)	Ponkan	China	China and Taiwan	Orlando Eustis Coconut Grove and Oneco Fla Riverside Calif	A large free peeling orange, early to midseason disease-resistant, highly esteemed in the Orient, for testing and breeding
	Clementine		Algeria	do	Reputed to be a natural hybrid of tangerine and sour orange but resembles tangerine, use in crosses with grapefruit gave rise to Clement tangelo
	Suen Kat (sour mandarin)	China	China	do	Serves as budding stock for best mandarin varieties of China and Formosa, being tested as stock for hardiness and disease resistance
	Changsha	do	do	Orlando Fla Fairhope Ala	Very hardy free-peeling orange promising for use in breeding
	Chin Kom	do	do	Orlando Fla	Not yet fruiting
	Sun Chu Sha	do	do	do	Do
	Hung Kat	do	do	do	Do
	Beauty (Ellendale) tangerine		Australia	do	To be tested for fruit quality, size, disease resistance and hardiness
	Vermilion tangerine	China	China	do	Do
C nobilis var *unshiu* (satsuma orange)	Kawano (early) also about 40 similar early maturing satsuma mutations	Japan	Japan	Fairhope and Silverhill, Ala Eustis, Fla (in part), Winter Haven, Tex (in part)	These large-fruited, early maturing satsuma varieties make possible earlier shipment of the commercial crop—avoiding frost risk and competition with tangerines Being tested for stock affinity, hardiness, stability of type, fruit quality also used in cross pollinations
	Ikiriki, Suzuki, Hiri Kashima Mizomoto, Miyasaki	do	do	do	Satsuma varieties of local fame in Japan, being tested for possible superiority to standard variety (Owari) in United States for hardiness, fruit quality, size of fruit, etc
C medica (citron)	Corsican, Spatafora Peretto, Java, Diamante, Chinese, Etrog	India	Italy, Sicily, Corsica Greece	Orlando Eustis Coconut Grove and Oneco, Fla Weslaco Tex Riverside, Calif	Varieties of citron adapted to the preserving industry are being tested for productiveness, disease resistance, and quality hybrids being made to improve existing forms Commercial citron growing has made a start in Florida, Puerto Rico, and California, but information is needed on stocks, varieties, disease resistance, etc There is a limited demand for the Etrog variety, used in certain Jewish ceremonials its form must accord with a fixed standard

TABLE 5.—*Citrus species and varieties introduced by the United States Department of Agriculture*—Continued

Species	Common or varietal name	Native habitat	Source of introduction	Where now available	Remarks
C. limonia (lemon)	India, Simla, Mazoe (wild types).	India, southeastern Asia.	India, South Africa	Orlando, Coconut Grove, and Eustis, Fla.	Testing importations in comparison with the "Florida rough lemon" for stock use and disease resistance.
	Algiers (seedless)	do	Algeria	Coconut Grove, Fla	Testing for adaptation to a humid climate, stock adaptability, and disease resistance.
	Meyer	China	China	Orlando and Eustis, Fla., Weslaco, Tex., Fairhope, Ala.	Testing for hardiness, stock adaptability, fruit quality, and disease resistance; also in hybridization work. This variety has been in commercial production for several years in Florida and the Gulf coast region; has proved quite hardy.
	Sumatra	Sumatra	Sumatra	Orlando, Fla., Weslaco, Tex	Not yet fruiting.
C. aurantifolia (lime)	Woglum	India, Malaysia, southeastern Asia.	India	Orlando and Coconut Grove, Fla.	Testing for seed content, fruit quality, productiveness, disease resistance; used in hybridizing.
	Giant, Cameron, Debe, Dominica.	do	West Indies	Orlando and Eustis, Fla	Tests of these introduced varieties indicate the names are local names for the common Mexican (or West Indian) lime, similar to the Florida Key lime.
	Sweet	do	Palestine	Orlando, Fla., Weslaco, Tex	Used to a limited extent as a stock; fruit insipid.
	Java	do	Java	do	Not yet fruiting.
C. mitis	Calamondin	Philippine Islands	China, Philippine Islands	Orlando, Eustis, and Coconut Grove, Fla., Weslaco, Tex., Fairhope, Ala.	A semihardy, limelike fruit, of possible use as a stock and serving as an excellent lime substitute. Crossed with the citrange it has given rise to an extra-hardy hybrid, the Glen citrangedin, an excellent "ade" fruit for the home fruit garden.
C. ichangensis		China	China	Orlando, Eustis, and Coconut Grove, Fla.	A very hardy form of citrus, of possible use as stock and for breeding purposes. "Ichang lemon", apparently a hybrid or large-fruited form.
C. junos Sieb	Yuzu	do	Japan	Orlando and Eustis, Fla	A hardy lemonlike form of citrus of possible use as a stock, as a lemon substitute in cool regions, and for breeding purposes.
C. hystrix		Philippine Islands, Malaysia.	Philippine Islands	Orlando, Coconut Grove, and Eustis, Fla., Summit, Canal Zone.	Fruits lemonlike but usually too aromatic to be edible; of possible use as stocks; not hardy.
	Kalpi	do	do	do	Fruits large, oblate, with edible lemonlike pulp; of vigorous growth; promising as a stock.

TABLE 6.—*Citrus relatives (Rutaceae) introduced by the United States Department of Agriculture*

Species	Common name	Native habitat	Source of introduction	Where now available	Remarks
Aegle marmelos (L.) Correa	Bael fruit	India	India	Orlando, Coconut Grove, Eustis, and Lake Alfred, Fla., Riverside, Calif., Mayaguez, P. R., Summit, Canal Zone	Deciduous, semihardy, producing an edible fruit, chiefly used in sherbet
Aeglopsis chevalieri Swingle		Tropical West Africa	West Africa	do	Fruit not edible, but for testing as stock
Atalantia citroides Pierre		Cochinchine	Cochinchine	Orlando, Lake Alfred, and Coconut Grove, Fla., Summit, Canal Zone, Mayaguez, P. R.	Fruit not edible, for testing as stock, decidedly ornamental—columnar habit, dark green foliage
A. disticha (Blanco) Merr., ***A. missionis*** (Wight) Oliv.	---	Cochinchine, Java	Java	Orlando, Fla.	Very resistant to salt and alkali, serves well as a stock for citrus species, decidedly promising for alkali or salty soils
Afraegle paniculata (Schum. and Thonn.) Engl., ***Balsamocitrus dawei*** Stapf, ***Afraegle gabonensis*** (Swingle) Engl.	"Powder pear	West Africa, central Africa, French Equatorial Africa	Original habitats	Orlando, Lake Alfred, and Coconut Grove, Fla., Summit, Canal Zone, Mayaguez, P. R.	Fruits not edible, of possible use as citrus stocks ornamental, not hardy
Swinglea glutinosa (Blanco) Merr.	Tabog	Philippine Islands	Philippine Islands	do	A large forest tree serves well as a citrus stock in warm soils, resistant to disease and vigorous
Chalcas koenigii (L.) Kurz		India	India	Orlando and Coconut Grove, Fla.	Foliage used extensively in the Orient for flavoring curries, readily propagated from root cuttings, useful as an ornamental, not hardy
Clausena lansium (Lour.) Skeels	Wampi	South China	South China	do	Fruit subacid, small, of good quality, of possible use as a stock, lemon buds readily on this stock but on other citrus species with difficulty
Citropsis schweinfurthii (Engl.) Swing. and M. Kell.	Cherry orange	Central Africa	Central Africa	Orlando, Lake Alfred, Coconut Grove, and Eustis, Fla., Riverside, Calif., Summit, Canal Zone	This species appears to be closely related to citrus, serves fairly well as a citrus stock in warm locations, resistant to common citrus diseases. The large compound leaves and numerous flowers make the tree decidedly ornamental
C. gabonensis (Engl.) Swingle and M. Kell.		French Equatorial Africa	Africa	do	Do
Eremocitrus glauca (Lindl.) Swingle	Desert kumquat	Australia	Australia	Orlando, and Eustis, Fla., Indio and Riverside, Calif., Sacaton, Ariz.	A xerophytic plant of possible use as a citrus stock in dry regions, a hybrid has been secured between this species and a citrange, which is of greatly increased vigor and may serve as a citrus stock

TABLE 6.—*Citrus relatives* (*Rutaceae*) *introduced by the United States Department of Agriculture*—Continued

Species	Common name	Native habitat	Source of introduction	Where now available	Remarks
Feronia limonia (L.) Swingle	Wood apple	India, Ceylon, Indo-China.	India	Orlando and Lake Alfred, Fla., Riverside, Calif., Summit, Canal Zone, Mayaguez, P. R.	Fruit used in preserves; tree useful as an ornamental in warm locations; also being tested as a stock.
Feroniella oblata Swingle	Krassang	Cambodia	Cambodia	do	Fruit used as a condiment.
F. lucida (Scheff.) Swingle	Kavista Batu	Java	Java	do	Fruits edible; both species of *Feroniella* ornamental and of possible use as a stock.
Fortunella hindsii (Champ.) Swingle.	Hong Kong kumquat	China	China	Orlando and Lake Alfred, Fla.	Fruits used as a condiment, but are very small and bitter; chiefly of interest as the plant has proved to be a tetraploid; crosses are being made with this species to secure seedlessness; one such cross, a triploid, has been secured.
Glycosmis pentaphylla (Retz.) Correa.		India, Indo-China	India	Orlando, Lake Alfred, and Coconut Grove, Fla., Summit, Canal Zone, Mayaguez, P. R.	Fruits small. Chiefly of use as an ornamental; not hardy.
Hesperethusa crenulata (Roxb.) M. Roem.	Naibel	Ceylon	Ceylon	Orlando and Lake Alfred, Fla., Summit, Canal Zone, Mayaguez, P. R., Eustis, Fla.	Fruits sometimes used as a condiment. Chiefly used as an ornamental. Stock tests gave unions with citrus, but not vigorous.
Laranga scandens (Roxb.) Buch. Ham.	Lavanga	India	India	Orlando and Lake Alfred, Fla., Summit, Canal Zone, Mayaguez, P. R.	Climbing shrubs.
Merrillia caloxylon (Ridley) Swingle.		do	do	Orlando and Coconut Grove, Fla.	Chiefly of value as an ornamental; not hardy.
Microcitrus australasica (F. Muell.) Swingle.	Finger lime	Australia	Australia	Orlando, Eustis, and Lake Alfred, Fla., Riverside, and Indio, Calif., Summit, Canal Zone, Mayaguez, P. R.	These Australian species are drought-resistant and are being tested as stocks. They are semihardy and useful as ornamentals. The fruits are scarcely edible, except possibly the last named, which has not yet fruited.
M. australis (Planch.) Swingle.	Dooja				
M. garrowayi (Bailey) Swingle.	Garroway's Finger lime.				
M. inodora (Bailey) Swingle	Russell River lime				
Paramignya monophylla Wight, *P. longipedunculata* Merr.		India	India	Orlando and Lake Alfred, Fla., Summit, Canal Zone, Mayaguez, P. R.	Climbing shrubs.
Poncirus trifoliata (L.) Raf.	Trifoliate orange	China	China	Orlando and Eustis, Fla., and Fairhope, Ala., Winter Haven, Tex.	This deciduous citrus relative is extremely hardy and useful as a stock in the northern limit of citrus culture, especially for the satsuma orange. Two forms have been noted, the normal small-flowered form and a large-flowered form of seemingly greater vigor. The trifoliate orange has been used in numerous hybrids, as the citranges and citrangequats.

Severinia buxifolia (Lam.) Ten.	"Box-leaved orange"	South China	South China	Orlando, and Eustis, Fla., Fairhope, Ala., Summit, Canal Zone, Mayaguez, P. R.	This shrubby tree is resistant to salt and may serve as a citrus stock. It is chiefly of use in ornamental hedge plantings. Several strains have been selected from imported seed of varying vigor and thorniness. Its immunity to citrus canker recommends it as a substitute in hedge plantings for the susceptible *Poncirus trifoliata*. Used as a dwarfing stock, it causes early flowering, hence is useful in hybridizing.
Triphasia trifolia (Burm. f.) P. Wils.	Lime berry	Unknown. (Widely distributed in tropical regions.)	Java	Orlando, Eustis, and Lake Alfred, Fla., Riverside, Calif., Summit, Canal Zone, Mayaguez, P. R.	A shrub or dwarf tree, chiefly of use as an ornamental; resistant to salt; fruits used sometimes in preserves.

Table 7.—*Summary of citrus breeding by the United States Department of Agriculture*

[Hybrids or selections introduced by the Department, 1892–1934]

Breeding procedure	Year introduced	Name of hybrid or variety	Parentage	Remarks
1. Hybridization through controlled cross-pollination:				
(a) Interspecific: F1 hybrids	1904	Sampson and Thornton tangelos.	Dancy tangerine × Bowen grapefruit.	These early introductions proved susceptible to scab and were poor shippers, with a short season of maturity.
	1931	Orlando (Lake), Seminole, Minneola, Yalaha tangelos.	do	This series of tangelos introduced in 1931 gave varieties high in quality, maturing from October to May, scab-resistant, and of good shipping quality.
	1931	Clement tangelo	Clementine tangerine × Bowen grapefruit.	A soft-fleshed hybrid for the home fruit garden; not recommended for commercial planting.
	1931	Umatilla tangelo	Satsuma orange × Ruby orange	Classed with the tangelo group which it resembles; very late maturing; scab-resistant.
	1931	Perrine lemon	Genoa lemon × Mexican lime	Fruit of size, shape, and quality of commercial lemon: highly resistant to scab and withertip; vigorous and productive.
F2 hybrids	1931	San Jacinto tangelo	Seedling segregate of an unnamed tangelo of little promise.	Adapted to conditions in the hot interior valleys of the Southwest, where most tangelos have been disappointing.
Backcrossing hybrids on parent variety.	1931	Wekiwa tangelo	Sampson tangelo × grapefruit.	Tree resembles pollen parent (Sampson) though less vigorous; fruit small, sweet, pink-fleshed, unlike either parent.
(b) Intergeneric. Bigeneric hybrids, F1 generation.	1904	Sanford, Rusk, Willitts, and Phelps citranges.	Trifoliate orange (*Poncirus trifoliata*) × sweet orange (*Citrus sinensis*).	The citranges with one exception (Rusk) had the trifoliate orange as the female parent. They failed in producing a hardy edible orange, owing to an excess of acrid oil in rind and pulp, but are proving useful as stocks and for further work in hybridization.
	1905	Morton citrange		
	1906	Colman, Rustic, and Savage citranges.		
	1911	Saunders and Cunningham citranges.		
	1923	Eustis and Lakeland limequats.	Mexican lime (*Citrus aurantifolia*) × round kumquat (*Fortunella japonica*).	The limequats have proved similar to the lime in fruit quality, but much hardier and resistant to lime withertip.
	1923	Tavares limequat	Lime × oval kumquat (*F. margarita*).	
	1932	Nippon kumquat, "orangequat".	Satsuma orange (*Citrus nobilis* var. *unshiu*) × Meiwa kumquat (*Fortunella crassifolia*).	This hybrid may be utilized in preserving like the kumquats, but is a much larger fruit borne on a more vigorous hardy tree. It also furnishes an excellent ade, owing to its acid, deep orange pulp.
Trigeneric hybrids, F1 generation.	1933	Thomasville and Telfair citrangequats.	Willitts citrange × oval kumquat (*Fortunella margarita*).	In these crosses the objectionable oil of the citrange is reduced so that the fruits may serve as hardy lime substitutes in making ade. The Thomasville also proved immune to citrus canker, a character derived from the kumquat parent.
	1933	Sinton citrangequat	Rusk citrange × oval kumquat.	

Table 7.—*Summary of citrus breeding by the United States Department of Agriculture*—Continued

[Hybrids or selections introduced by the Department, 1892–1934]

Breeding procedure	Year introduced	Name of hybrid or variety	Parentage	Remarks
Trigeneric hybrids, F_1 generationr	1931	Glen citrangedin	Willitts citrange × calamondin (*Citrus mitis*).	In this cross the objectionable oil content of the citrange is eliminated, giving rise to an ade fruit similar to the calamondin but much more hardy.
2. Selection: (a) Seedlings (apogamic or nonhybrid).	1904	Weshart and Trimble tangerines.	Derived from Dancy cross-pollinated seed, but not hybrids.	Seedlings exhibiting apparently extra vigor and producing fruits of larger size than the parent variety.
	1905 1906	Everglade lime Palmetto lime	Grown from lime seed from cross-pollinated fruits, but not hybrids.	Apparently extra vigorous strains of the Mexican lime with some indications of withertip resistance.
	1912	Davis (Little River) grapefruit.	Original seedling from cross-pollinated fruit of a seedy grapefruit (with Dancy tangerine pollen); not a hybrid.	This seedling produced a new type of seedless grapefruit (4-6 seeds) with the fruit quality of the seedy grapefruit; indications are that it is a superior canning variety.
	1931	Silverhill satsuma orange.	Original seedling from cross-pollinated Owari satsuma (sweet orange pollen), but not a hybrid.	This variety exhibits extra vigor and hardiness, with large-sized fruit of good quality.
	1932	Oklawaha sour orange	Derived from cross-pollinated sour orange (sour pummelo pollen used), but not a hybrid.	Tree of vigorous productive character with large thick rind fruits adapted to use in marmalade preparation. This character has been transmitted in budded progeny.
Bud selection [1]	1921-36	Valencia, Lue (Lue Gim Gong), Pineapple, Parson Brown, and Homosassa oranges; King mandarin; Dancy and Oneco tangerines; Marsh, Duncan, Hall, Davis, Foster, and Thompson grapefruit	Budwood secured from performance record trees; several progeny rows of each variety budded and grown under uniform conditions with record of yield, and special attention to the production of any off-type fruit. (1 progeny of Lue was discarded and replaced, owing to tendency to produce ridged fruits. A bud sport of the Parson Brown has been studied over a period of years and seems to be a chimeral mutation).	Under the terms of the cooperative agreement the disposition of budwood from the progeny grove is in the hands of the Florida Agricultural Experiment Station, and considerable demand has developed in recent years among growers and nurserymen for this true-to-type budwood of standard varieties. The experiment station, also under the cooperative agreement, is testing the new citrus hybrids introduced by the Department and maintains a collection of the citrus relatives furnished by the Department.

[1] Standard orange varieties as listed by the standardization committee of the Florida Citrus Seminar 1916; other citrus varieties selected and propagated in cooperation with the Florida Agricultural Experiment Station at the Citrus Experimental Station, Lake Alfred, Fla. For bud selection work in California, see table 8.

TABLE 8.—*Bud mutations in citrus discovered by Shamel and coworkers, of the United States Department of Agriculture, in cooperation with the California Citrus Experiment Station, Riverside, Calif., 1909–36*

SWEET ORANGE (WASHINGTON NAVEL STRAINS)

Strains	Characteristics	Date discovered	Remarks
Superior strains:			
Improved Washington.	Uniformly heavy production of uniformly desirable oranges.	1909	1,402,950 selected buds sold by Fruit Growers Supply Co. and estimated 2,000,000 otherwise distributed.
Robertson	Early maturity, resistant to "June drop."	1925	Plant patent 126.
Inferior strains:			
Thomson	Fruits generally lacking juice and flavor.	1909	Propagated sparingly in few districts.
Unproductive	Very low production	1913	Trees top-worked to Improved Washington.
Australian	Low production, poor fruit, rank growth.	1909	Do.
Willow-Leaf	Narrow leaves, small fruit	1915	Do.
Dry	Very little or no juice	1914	Do.
Yellow	Pale yellowish color of peel	1909	Do.
Brown-Spotted	Sunken brown spots on peel	1915	Do.
Golden Buckeye	Lacking in juice	1909	Do.
Golden Nugget	Lacking in juice; pale color of peel	1909	Do.
Dual	Uneven texture of rind	1914	Do.
Corrugated	Deeply and uniformly ridged fruit	1909	Do.
Ribbed	Shallow and uniformly ridged peel	1909	Do.
Seamed	Very shallow, narrowly seamed peel	1914	Do.
Fluted	Broadly and evenly ridged peel	1910	Do.
Flattened	Flattened shape of fruit	1909	Do.
Pear-Shape	Pyriform shape of fruit	1909	Do.
Elliptical	Oval shape of fruit	1909	Do.
Sheepnose	Small, pear-shaped fruit, enclosed navels.	1915	Do.
Rolled-Leaf	Rolled leaves, unproductive	1921	Do.
Minor importance	Many strains of minor economic importance but originating from bud mutations.	1909–36	Do.

SWEET ORANGE (VALENCIA STRAINS)

Strains	Characteristics	Date discovered	Remarks
Superior strain:			
Improved Valencia	Uniformly heavy production, uniformly good quality of fruit.	1912	2,337,000 selected buds sold by Fruit Growers Supply Co., and estimated 2,250,000 buds otherwise distributed.
Inferior strains:			
Unproductive	Very low yields	1912	Trees top-worked to Improved Valencia.
Willow-Leaf	Narrow leaves, small fruits	1912	Do.
Dwarf	Small tree, low yields	1912	Do.
Persistent-Style	Style tends to remain with fruit	1915	Do.
Flattened	Flattened shape of fruit	1912	Do.
Long	Long or oblong shape of fruit	1912	Do.
Fluted	Broadly, evenly, and smoothly ribbed fruit.	1912	Do.
Corrugated	Deeply ridged, rough texture of rinds	1912	Do.
Ridged	Sharply and unevenly ridged rinds	1912	Do.
Coarse	Coarse, rough texture of rinds	1912	Do.
Yellow	Pale color of peel	1912	Do.
Misshapen-Leaf	Irregularly shaped leaves, low yields	1914	Do.
Small Smooth	Very small fruit, smooth, very thin rinds.	1912	Do.
Variegated	Leaves light and dark green	1915	Do.
Minor strains	Many economically unimportant strains differing in tree and fruit characteristics from all others.	1912–36	Do.

LEMON (EUREKA STRAINS)

Strains	Characteristics	Date discovered	Remarks
Superior strain:			
Improved Eureka	Heavy yields of uniformly good lemons.	1911	767,000 selected buds sold by Fruit Growers Supply Co., and estimated 1,250,000 buds otherwise distributed.

TABLE 8.—*Bud mutations in citrus discovered by Shamel and coworkers, of the United States Department of Agriculture, in cooperation with the California Citrus Experiment Station, Riverside, Calif., 1909–36*—Continued

LEMON (EUREKA STRAINS)—Continued

Strains	Characteristics	Date discovered	Remarks
Inferior strains:			
Small-open	Small-sized fruits	1911	Trees top-worked to Improved Eureka.
Pear-shape	Pyriform-shaped fruits	1911	Do.
Shade-tree	Vigorous tree growth; coarse, thick rinds.	1911	Do.
Unproductive	Very low yields.	1911	Do.
Corrugated	Strongly ridged and coarse-textured rinds.	1911	Do.
Ribbed	Evenly ribbed texture of rinds	1911	Do.
Variegated	Leaves light and dark green, fruits ridged.	1912	Do.
Striped	Light stripes on fruits	1912	Do.
Crumpled leaf	Crumpled appearing leaves, low yields.	1911	Do.
Minor strains	Many strains originating from bud mutations of minor economic importance.	1911-36	Do.

LEMON (LISBON STRAINS)

Strains	Characteristics	Date discovered	Remarks
Superior strains:			
Improved Lisbon	Heavy production of uniformly desirable fruits.	1913	86,215 selected buds sold by Fruit Growers Supply Co., and estimated 125,000 buds otherwise distributed.
Dense-productive	Vigorous growth, resistant to wind damage.	1913	Do.
Inferior strains:			
Open	Spreading tree growth, susceptible to sunburn.	1913	Trees top-worked to Improved Lisbon.
Unproductive	Very low yields	1913	Do.
Ribbed	Ridged texture of rind	1913	Do.
Corrugated	Heavily ridged and very coarse-textured rinds.	1913	Do.
Collared	Bottle-shaped with necked stem ends.	1913	Do.
Striped	Light-colored stripes on rinds	1913	Do.
Thornless	No thorns	1920	Do.
Minor strains	Many strains of minor commercial importance but of scientific interest.	1913-36	Do.

GRAPEFRUIT (MARSH STRAINS)

Strains	Characteristics	Date discovered	Remarks
Superior strains:			
Improved marsh	Heavy production of uniformly desirable fruits.	1910	1,262,757 buds sold by Fruit Growers Supply Co. and estimated 750,000 buds otherwise distributed.
Dawn	Early maturity of fruits	1927	
Inferior strains:			
Corrugated	Ridged texture of rinds	1910	Trees topworked to Improved Marsh.
Seedy	Excessive number of seeds	1910	Do.
Pear shape	Pyriform-shaped fruits	1910	Do.
Minor strains	Several strains of minor commercial importance but of scientific interest.	1910-37	Do.

TANGERINE (DANCY STRAIN)

Strains	Characteristics	Date discovered	Remarks
Superior strain:			
Improved Dancy	More regularly productive	1915	56,973 selected buds sold by Fruit Growers Supply Co.

TABLE 8.—*Bud mutations in citrus discovered by Shamel and coworkers, of the United States Department of Agriculture, in cooperation with the California Citrus Experiment Station, Riverside, Calif., 1909–36*—Continued

LIME STRAINS

Strains	Characteristics	Date discovered	Remarks
Superior strains:			
Improved Mexican	Selected for size of fruits	1924	5,163 selected buds sold by Fruit Growers Supply Co.
Improved Bearss	Selected for heavier production	1928	

NOTE.—*The article entitled Improvement of Subtropical Fruits other than Citrus, by Hamilton P. Traub and T. Ralph Robinson, appears in the 1937 Yearbook Separate on Improvement of Subtropical Fruits.*

NUT BREEDING

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IMPROVEMENT in nuts by some sort of selection was probably brought about originally by cave men, wild animals, and birds. The more toothsome nuts were the ones chiefly sought after and carried from place to place or hidden in caches. Weaker creatures, forced by stronger rivals from warmer and more comfortable localities, were obliged to steal their food and carry it to places safer for themselves although often less favorable for the nuts, which they might lose, to take root and thrive. It was by such means that the productive areas were gradually expanded and greater hardiness and ability to grow at higher or lower altitudes were developed. Ocean currents, which have much to do with the distribution of many kinds of seeds, appear to have had little part in the carrying of Temperate Zone nuts from place to place.

Planters have as yet made little systematic effort to breed superior varieties of any kind of nuts by hybridization. This is doubtless because of the great abundance of wild nuts that in the past could be had for the gathering, and more recently because of the practical difficulties standing in the way of tree breeding, especially the time required to complete the cycle of a generation. The countless centuries of crude selection through which such cultivated forms as filberts, almonds, Persian (English) walnuts, and European chestnuts have passed have tended so to fix the types that to a large extent they now come fairly true to type from seed, although in this country none but grafted trees of selected varieties are planted, except when only seedlings are to be had. Most of the nuts now on the world market are from seedling trees. The extensive multiplication of superior varieties resulting from selective or controlled breeding is still greatly handicapped by practical difficulties in propagation, especially in the case of the more difficult species of walnut and hickory.

CHESTNUT

CHESTNUT improvement in this country has developed along four distinct lines—by selection from native seedlings, by the introduction of Old World species and the continuance of selection with them, by natural hybridization among various species and varieties when grown together, and by controlled hybridization, the newest and most promising method.

Breeding by selection from native species has contributed little, as few varieties developed by this method have become prominent.

The majority so originated are now obsolete, and it would probably be impossible to establish the purity of the supposed American parentage of the very few still grown by nurserymen. Numbers of hybrids exist that are plainly the result of natural crossing between native species, but none has commercial value.

Because the American chestnut is very susceptible to what is known as blight, a fatal fungus disease from the Orient, which was first discovered in this country in 1904 and has since spread over practically the entire East, the chief interest in chestnut planting now lies in the use of species from the Old World.

Altogether eight species of chestnuts, including the closely related chinquapins, have been used in the chestnut developments of this country. Formerly the most important and abundant of these species was the American chestnut, *Castanea dentata* (Marsh.) Borkh. This had a natural range extending from lower New England westward to southeastern Michigan and southward to northern Georgia and eastern Arkansas. As a tree it was one of the largest growing species of the Eastern States; a trunk diameter of 6 to 7 feet and a limb spread of 50 or more feet from the center of the tree were not uncommon with trees standing in the open. As a forest tree it was once a dominant species over large mountain areas of the Appalachian Range from Pennsylvania south to the Carolinas and eastern Tennessee. In these regions a height of more than 100 feet with a diameter at the base of

WHEN *the chestnut blight wiped out this magnificent eastern forest tree in the early part of the present century, chestnut breeding became a pressing need. The most promising of all material at present is the Chinese chestnut. It is much more blight-resistant than any others, and the nuts combine the large size of the European chestnut with the sweetness of the American. The Japanese chestnut, which has considerable blight resistance, unfortunately produces nuts that are usually negative in flavor, but it may be useful in breeding. Selection and hybridization are being actively carried on by the Department of Agriculture with the object of developing varieties for both commercial and home growing that will be resistant to blight and if possible to weevils, and hardy enough to grow throughout the chestnut range; bear heavy annual crops, beginning at a fairly young age; bear not more than three rather large nuts to the bur, which must separate automatically; have fine texture, good flavor, and good keeping quality; be attractive in appearance and not subject to shell splitting; and have an inner skin or pellicle that will not adhere to the kernel.*

not more than 2 to 3 feet was common. The trees were much sought after as material for telephone poles, fence rails, mine props, and other similar purposes where important factors were abundance, uniformity of size, freedom from knots, ease of splitting, and durability both above and below ground.

The burs of the American chestnut are relatively large and the spines long and compound. The nuts are coated at the apex, or nearly to the middle, with thick, pale down. The kernels are very sweet and palatable. Selected nuts of this species are among the most delicious of any known. They were thought to be the choicest of all chestnuts until the arrival of certain oriental strains, which proved to be their equal.

Two other species of *Castanea* are indigenous to this country. Both are chinquapins and therefore not true chestnuts, although closely related. These are much alike and are restricted to more limited ranges than the American chestnut. The trees are dwarfish or shrubby in habit, and the nuts are borne singly in small burs, which form in racemes or long, stringlike clusters. The nuts are small but very sweet. The better known of the two species is the tree or common chinquapin, *C. pumila* (L.) Mill. This occurs chiefly in the Southeast, from central Pennsylvania to Florida and west to Texas. The species occasionally forms hybrids with the American chestnut. One such hybrid tree was found, probably about 1895, by the late J. G. Rush, of West Willow, Pa. This was propagated and disseminated to some extent by Rush, after whom it had been named, but after a few years of experimentation he cut down the trees as he came to regard the variety as merely a novelty of little practical value. However, trees are still grown by some who find it an interesting form of considerable value for home use. The other species of chinquapin is the so-called alder-leaved or trailing chinquapin, *C. alnifolia* Nutt., a low-growing shrub confined to certain localities in the South Atlantic States and occurring rarely as far west as central Louisiana. This species has the peculiarity of reproducing itself by means of underground stems and forming dense thickets.

Developments From Early Introductions

The first foreign chestnut introduced into this country was the European or Spanish chestnut, *Castanea sativa* Mill. The earliest record that has so far come to light appears in the notes of Thomas Jefferson, according to Bailey (*5*),[1] and shows that scions of a "French chestnut" were grafted by him in 1773 at his home, Monticello, near Charlottesville, Va. This species also is a large tree, growing in Europe to 100 feet in height and 30 feet in circumference, though in this country it seldom grows larger than a medium-sized apple tree. The trees are precocious and under American conditions very fruitful. The nuts are large and usually very good but rarely equal in quality to the average American chestnut. The tree is scarcely less fatally subject to blight than the American chestnut and therefore is not longer being planted in blight-affected zones.

The second foreign species to become important in this country was the Japanese chestnut, *Castanea crenata* Sieb. and Zucc. This is a

[1] Italic numbers in parentheses refer to Literature Cited, p. 881.

relatively small tree or shrub growing to 30 feet in height. The species is characterized by small stiff leaves, great fruitfulness, and large size of nuts, which are sometimes enormous. Occasionally the nuts are very good but as a rule the flavor is mild or neutral and the texture somewhat coarse. Quite commonly the pellicle or skin covering the kernel is thick or even woody. It may adhere tightly and be removable only by paring with a knife. The species is quite resistant to blight, although in the experience of the Division of Forest Pathology, Bureau of Plant Industry, United States Department of Agriculture, it is exceeded somewhat in this respect by the Chinese or hairy chestnut (*C. mollissima* Bl.)

The Chinese chestnut tree is intermediate in size between the European species as grown in this country and the American species. It was known in the United States to a slight extent as early as 1853, but it may be said to have been introduced by the Department of Agriculture in 1907. While very young it tends to develop many lateral branches with little tendency toward a central leader. Later on it assumes more definite shape and becomes a standard tree. It begins bearing relatively early and is sometimes highly prolific. The outstanding feature of this species, in addition to the fact that it is apparently more resistant to blight than any other, is the excellence of the nuts, many of which are as large as the European and as sweet as the best American nuts They are attractive in appearance, often being of a rich mahogany brown and frequently glossy. There is little down on the surface and that only at the apex. When in the proper stage of maturity the pellicle of the kernels tends to adhere to the shells rather than the kernels

In 1799 Irenée du Pont came to New Jersey from France and "after a residence at Bergen Point, where he took much pleasure in propagating a number of European seeds and plants received from France, removed to Delaware in 1802 and settled on the Brandywine, where he established the famous Du Pont Powder Mills" (*26*). At both places Du Pont paid special attention to bringing European chestnuts into this country, chiefly from his native home, and to disseminating both these and their offspring among his friends and acquaintances. Records show that many varieties of European chestnuts, which during the eighties and nineties became prominent in this country, were derived from Du Pont introductions

Powell (*26*) records that scions taken from one of the Du Pont trees and grafted in 1850 on stocks of the native species gave rise to a variety named Darlington, after Thomas Darlington, of West Chester, Pa., who was intrumental in disseminating the variety. This may have been the first chestnut grafting in this country after that of Jefferson.

Beginning in the early eighties and continuing for about two decades, a large number of seedlings of European species were named and propagated. Some of these were popularly supposed to have been hybrids with the American species, but this was not proved. A few were extensively used in top-working coppice growth in cut-over chestnut forest lands of eastern Pennsylvania, New Jersey, northern Maryland, and northern Virginia. All proved to be fatally susceptible to blight. The best-known varieties were Paragon, Numbo,

Ridgeley, Cooper, and Scott. These are now rarely grown and are found only in districts outside of blight-affected zones. Even there they are being replaced by better varieties.

A more recent group of varieties, thought by some to be partially or entirely European in origin, although regarded by the originator as pure American, was developed by the late E. A. Riehl, of Godfrey, Ill., from seedlings of unknown origin obtained from the nursery of Charles A. Green, Rochester, N. Y., and planted about 1890. To hasten the trees into early bearing Riehl grafted scions from them into the top of an old seedling American chestnut. The resulting nuts so impressed him that he named the variety Rochester. From Rochester seedlings he selected and named a number of still better varieties such as Progress, Fuller, Champion, and Van Fleet. Gibbens, from the same source, has been added since Riehl's death in 1924. However, these varieties, like all others having either European or American parentage, are very susceptible to blight, and when once affected the trees perish quickly.

The Japanese chestnut, *Castanea crenata*, has also been a source of numerous varieties having desirable characteristics. According to Fuller (*14*), the earliest recorded introduction of this species took place in 1876, when a number of trees were received by S. B. Parsons & Co., nurserymen at Flushing, N. Y., from Thomas Hogg, a skilled horticulturist of this country who spent several years in Japan collecting rare kinds of trees and shrubs. These trees fruited in 1878 and soon attracted attention on account of the large size and excellent quality of the nuts and their precocious bearing habits. According to Powell (*26*), "Parson's Japan" was well known for a few years, but presently disappeared.

In 1882 the late William Parry, of Parry, N. J., imported 1,000 grafted trees from Japan, and from them a single tree, the Parry, was finally selected and became the progenitor of many varieties. In 1886 Luther Burbank, of Santa Rosa, Calif., planted large Japanese chestnuts collected for him in Japan, and from over 10,000 bearing seedlings he selected 3 as worthy of perpetuation—Hale, Coe, and McFarland. In 1915 he introduced another variety, Miracle, also of Japanese origin. Groups of Japanese varieties were developed by J. W. Kerr, Denton, Md., and J. W. Killen, Felton, Del., probably from seed procured from Parry or other importers. Each of these men introduced a considerable number of carefully chosen varieties, of which Black, Felton, Kent, Kerr, Killen, and Martin are still being grown occasionally on the Chesapeake Peninsula.

Developments and extensive plantings of Japanese and European chestnut varieties made from 30 to 40 years ago included those of the Albion Chestnut Co. at Clementon, N. J.; the Mammoth Chestnut Co. and Joseph Williams at Riverton, N. J.; Joseph T. Lovett at Emilie, Pa.; the Paragon Nut & Fruit Co., Lancaster, Pa.; and C. K. Sober, Lewisburg, Pa.

Breeding by Hybridization

Chestnut breeding by controlled cross-pollination appears to have been the first work of the kind undertaken in this country, if not in the world, with any species of nut, and a number of apparently good

varieties were so developed. Unfortunately, chestnut blight entered from the Orient at about the time the hybrids were ready to be introduced, and none proved to have sufficient resistance to this disease to justify extensive planting. This early work was undertaken almost simultaneously by two men wholly unknown to each other and living in remote sections of the country. Both died about the time that material was becoming available with which the next steps in breeding and the development of blight-resistant varieties might have been taken.

The first work appears to have been that begun in 1888 by George W. Endicott, of Villa Ridge, Ill., a veteran of the Civil War, farmer, and practical fruit grower. In that year he began a search for an American chestnut tree blossoming early enough to furnish pollen for use on the pistillate flowers of the Giant (Japan Giant) variety (*39*), which was prolific but not of high grade. It was as a result of such a cross made by him in 1895 that he developed the Boone variety.

The next hybridizing work with chestnuts began in 1894 when Van Fleet (*43*) well known in this country as a breeder of roses and small fruits, who was then an associate editor of the Rural New Yorker, dusted pollen of a native chestnut on the pistillate flowers of Paragon, a popular variety of European parentage. The resulting seedlings were grown on the private grounds of Van Fleet in Little Silver, N. J. Coming into bearing in 1906, they showed unmistakable signs of hybridity and might have become valuable had they not been seriously attacked by chestnut blight a year or so after beginning to fruit.

The period of Van Fleet's most important work in chestnut breeding began in 1900. Between then and the time of his death in 1921 he made thousands of crosses, using many species and growing hybrids through several successive generations. His earlier work largely consisted of crossing the native chinquapin, *Castanea pumila*, with such leading European varieties as Numbo and Paragon and such Japanese sorts as Parry (Parry's Giant), Killen, and Hale. To some extent he also used pollen from native wild trees of the American chestnut. In his later work he included the Chinese chestnut, *C. mollissima*.

The final results of Van Fleet's work were practically nil, so far as production of commercial varieties was concerned, for the reason that all hybrids having any degree of either American or European parentage proved susceptible to blight and soon succumbed. However, one hybrid, designated as S–8 from its position in the orchard, and believed to have been the result of a cross of chinquapin with Japanese chestnut, is being tested under controlled infection conditions for possible resistance. Recent reports indicate that this hybrid is not sufficiently resistant to blight to justify general planting.

The work of both Endicott and Van Fleet is important because it gave information as to the possibility of using different species in breeding and it developed a useful technique.

The chestnut breeding of Van Fleet has been continued and expanded by the Division of Forest Pathology of the Bureau of Plant Industry with G. F. Gravatt and R. B. Clapper in charge. Thousands of crosses have been made involving the eight species, and the work has been carried through several successive generations. Selections are now being made of the most promising individuals for varietal use.

Defects and Merits of Present Varieties

Present varieties of the chestnut have many serious defects, of which susceptibility to certain natural enemies is most prominent. One of these enemies is chestnut blight, the fungus disease already referred to as attacking all species in varying degrees. It has spread rapidly over the native range of the chestnut since it was first discovered on Long Island early in the present century. It is most serious with the American and next with the European chestnut. Japanese varieties and seedlings are resistant. Varieties of the Chinese chestnut, *Castanea mollissima,* appear to be even more resistant, and as the nuts are generally superior to those of the Japanese chestnut, the species appears to offer greater promise for orchard planting.

Chestnut weevils are native pests attacking all choice varieties with about equal severity. If any chestnuts are less subject to this menace than others they are the largest and least palatable of those from Japan. The adult weevil deposits its eggs deep in the immature kernel when the nut is partially grown. One egg or many may be placed in each nut. They hatch at about the time the nuts ripen, and the larvae feed and fatten inside the nut, then bore their way out and enter the ground for the winter stage. In early-ripening varieties these insects often do not appear until after the nuts have arrived in the market. A few days later, especially if the weather is warm, and about the time the nuts reach the consumer, the white larvae or grub-like insects emerge. In severe infestations these pests will be seen crawling in all directions, or if a nut is cut open they will be found in various parts of the kernel, to the disgust of the would-be consumer.

Whether blight, which may completely kill the tree and end the story, or weevils, which do not affect the tree but ruin the nuts after they are grown, is the more seriously limiting factor in chestnut growing is an open question. No method of spraying has been found sufficiently effective with either to be worth while. However, as already stated, the blight-resistant Chinese and Japanese species appear to offer a practical solution to the former evil, and to some extent planting chestnut trees only in thickly populated poultry yards is being found successful in controlling the latter. One way of avoiding weevil damage would be to plant only in parts of the country where this pest is not known to be present. As time goes on, more satisfactory means of controlling or obviating both of these natural enemies may be developed.

Other defects of chestnuts are tardy bearing; shy bearing or over-productiveness; lateness in time of maturity; failure of the burs to open and discharge the nuts automatically; variability in size of nuts; a tendency for the shells to split badly and thus expose the kernel to weather; thickness of pellicle; tight adherence of pellicle to the kernel; and coarseness, lack of sweetness, and poor keeping qualities. No known varieties are free from all of these objectionable features. With some exceptions, the American chestnut bears nuts that are small and unattractive in appearance, and the pellicle of the kernel adheres tightly, although it is so thin as not to be objectionable. The trees grow to immense size but are tardy in beginning to bear and seldom bear

heavily. Besides being fatally subject to blight, the European chestnut is usually of medium flavor, the pellicle adheres tightly to the kernel, and the texture is seldom as fine as that of the American and Chinese species. The chief defects of the Japanese chestnut are poor flavor and coarseness of kernel, thickness and even woodiness of pellicle, and usually tight adherence of pellicle to kernel. As a rule Japanese chestnuts are good to eat only when cooked. The Chinese chestnut also has its defects, but owing to its newness in this country it has not yet been fully appraised. As already noted, it is subject to weevils and somewhat so to blight. Young trees are slow in assuming distinct tree form. While of nursery age the little trees are very subject to winter injury. Nothing is known as to the self-sterility or inter-sterility of Chinese varieties. Very few have yet been named and none has been thoroughly tested. The real merits and defects of this species can be determined only by wide observation over a period of years.

The good characteristics of chestnuts are fairly well distributed among the various species and varieties. The American chestnut makes the largest and most upright tree, is by far the best for timber purposes, and the kernels are the most uniformly sweet. The European chestnut bears well and annually, beginning at a moderately early age. The tree does not ordinarily assume such great size as to be objectionable to the orchardist. The nuts are of good commercial size, and those of some varieties are sweet and highly palatable. Nuts of this species often bring top prices. The Japanese chestnut is outstanding in its normal precocity, prolificacy, habit of annual bearing, and large size and attractive appearance of the nuts. The species is highly resistant to blight and would need only the sweetness, fineness of texture, and palatability of the best American and Chinese chestnuts, and the automatic separation of pellicle from kernel, characteristic of some of the latter, to rank among the favorites with both growers and consumers. There are a few Japanese varieties of such merit as to give promise of orchard usefulness.

As a rule, all chestnuts are more or less self-sterile and bear better when interplanted with other varieties or seedlings.

The Chinese chestnut appears at this time to offer the greatest opportunity for improvement by breeding. The trees do not attain the large size of the American species, which is undesirable, but they do become somewhat larger than the Japanese, which in this country seldom exceed the apple tree in size. The Chinese chestnut is highly resistant to blight, and so far as observed the best seedlings and varieties bear freely without being overproductive. Some of the heaviest-bearing trees of this species in a seedling orchard located at the United Station Pecan Field Station, Albany, Ga., now 10 or 12 years of age, are annually producing from 50 to 70 pounds of nuts each. The finest nuts of the Chinese species are about all that could be desired. The largest are equal in size to the average chestnuts imported from Italy as commonly seen in eastern cities from midfall until after the holidays. Typically the Chinese chestnuts are of dark, chocolate-brown color, overlain with thick to thin gray or whitish down that may cover the greater part of the exposed surface or be confined to a small area immediately surrounding the apex. They are commonly glossy and attractive. Some are only mildly sweet, but others are excellent.

With regard to automatic separation of nuts from the burs, as well as time of maturity of crop, marked variability exists among seedlings and varieties of all species. As a rule the Chinese and Japanese chestnuts ripen earlier and separate themselves from the burs better than either European or American chestnuts.

Present Breeding Work

Breeding work is largely confined to the Chinese chestnuts, though the Japanese may be useful to some extent. The present work in improving the Chinese chestnut necessarily involves the selection of seedlings promising as new varieties and the use of such varieties in actual breeding by hybridization. During the past several years the United States Department of Agriculture, Bureau of Plant Industry, through its Divisions of Fruit and Vegetable Crops and Diseases and of Forest Pathology, has examined nuts from several hundred trees in various parts of the country. Probably 100 seedlings are now under observation. Scions of many of the best have been grafted upon nursery stocks and are now on their way to early bearing. Three of the trees tentatively selected in 1930 have been propagated by individuals outside the Department and to some extent are being commercialized, although they are by no means fully tested or approved by the Bureau. One of these is known as Carr, after R. D. Carr, Magnolia, N. C., to whom the original tree was sent by the Bureau in 1919. Another is Hobson, so called after James Hobson, Jasper, Ga., to whom, with a number of others, it was sent in 1919. The third variety is Zimmerman. This was selected by the Bureau from a lot of seedlings grown by G. A. Zimmerman from nuts imported by him in 1924 through Nanking University, Nanking, China.

The trees under observation also include a number of Japanese seedlings that now appear to be of considerable promise. The majority of these are of recent origin, as they were brought to light in 1929 as a result of cash prizes financed that year by John Harvey Kellogg, Battle Creek, Mich., through the Northern Nut Growers' Association.

The aims in breeding are to produce varieties that will be of value for the general market or the home or both. The desired characteristics at present are resistance to blight and weevils, heavy annual bearing, moderate precocity, early and quick maturity of nuts ahead of frosts, automatic separation of the nut from the burs, not more than three nuts to the bur, large but not of too great size, attractive appearance, freedom from shell splitting, thinness of pellicle, automatic separation of kernel from pellicle, fine texture, good flavor, and good keeping quality. Hardiness in all parts of the native or adapted range of the chestnut is also important.

In the appendix will be found a list of persons now engaged in the improvement of the chestnut through breeding.

FILBERT

The term "filbert" is used in this article in accordance with the popular American usage and is understood to imply a superior type of nut of the botanical genus *Corylus*. The term "hazel" is used for the inferior and smaller nuts. In Europe the distinction is drawn upon the basis

of length of husk in proportion to that of the nuts. Those that have husks no longer than the nuts are called hazels, while those with husks longer than the nuts are called filberts. This distinction is difficult to follow, once the husks have been removed.

At least four species of *Corylus* are under cultivation for nut production. Two of these are tree forms attaining a height of 80 to 125 feet. Both are commonly called hazels, as the nuts they bear are rather small, thick-shelled, and inferior in edibility. One is the Turkish or Constantinople hazel, *C. colurna* L., of southeastern Europe and western Asia. According to Rehder (*28*), this species was introduced in 1853. It is extremely hardy, doing well in western New York, where three fine trees 50 feet tall are to be seen in Highland Park, Rochester. It is used in this country for ornamental planting and as a stock on which to graft superior varieties of the European filbert. The latter use is still in the experimental stage and is not recommended for commercial purposes. The other tree species is the Chinese hazel, *C. chinensis* Franch., which Rehder states was introduced into this country in 1895. Its usefulness for stock or other purposes has not yet been determined.

Two native species of *Corylus* that are being used to some slight extent in the development of varieties are the eastern hazel, *C. americana* Marsh., and the beaked hazel, *C. cornuta* Marsh. Both are shrubby species producing nuts ordinarily of little value. The former has much the greater range in this country, as it is common from the Lakes to the Gulf, whereas the latter occurs only in the northernmost States. Nuts of the eastern hazel have husks longer than the nuts, and they develop as overlapping valves opening at one or both sides to the base. The beaked hazel has long, tubular, and thickly spiny husks, which remain tightly closed. A form found on the Pacific coast, greatly resembling the latter and known by some authorities as *C. californica* Rose, but by others as a form of *C. cornuta*, is common as a wild shrub from California north to Washington. This has been used little or not at all in breeding work. A number of varieties of *C. americana* have been introduced into garden culture in the East and are being grown by nurserymen. The three best known are Rush from Pennsylvania, Littlepage from Indiana, and Winkler from Iowa. Rush has been used extensively in breeding new hybrid varieties. Littlepage and Winkler have been used to some extent in this way.

The commercial production of filberts is now an important industry in the Pacific Northwest, especially in the Willamette Valley of Oregon and in nearby parts of western Washington. Most of the varieties are of the species *Corylus avellana* L., although some are of *C. maxima* Mill. and others are apparently hybrids between these two species. Trees of the former often attain heights of 25 to 30 feet, and many of those first planted in this country now have trunks fully 18 inches in diameter a foot or so above ground. Those of the latter are said to attain a height of 30 to 35 feet in Europe and Asia, but no trees of such size are known in this country. The husks may be shorter or longer than the nuts, or of the same length. All cultivated varieties except those of *C. maxima* parentage have husks that are open or overlapping at the sides. The husks of *C. maxima* varieties

remain tightly closed. The nuts may or may not be naturally discharged free from the husks; varieties of *C. avellana* vary greatly in this respect. Typical varieties of *C. avellana* are Barcelona, Bolwyller, Du Chilly, Daviana, and Italian Red. White Aveline is the best known variety of *C. maxima* parentage.

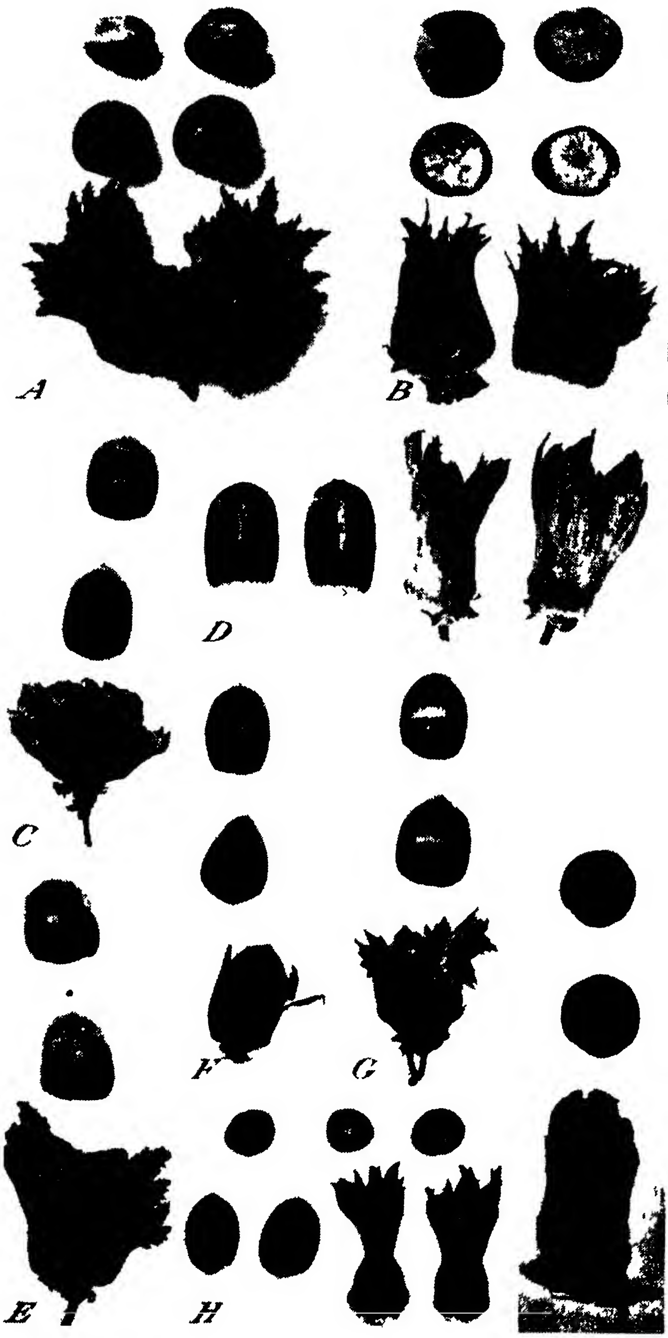
Need for Cross-Pollination

As far as known all varieties of *Corylus* are self-sterile and must be interplanted in order to assure effective pollination, a fact that is of rather recent discovery, although it became known more than a century ago that varieties are often made more fruitful by the application of additional pollen from other trees to the pistillate flowers of those having a scarcity of staminate flowers. This appears to have been the discovery of George Swayne of England about 1821. He discussed it at some length in a paper On the Fertilization of the Female Blossoms of Filberts, which he read February 18, 1823. The paper was published the following year in the Transactions of the Horticultural Society of London.

Figure 1.—John Franklin Jones (1871–1928), Lancaster, Pa., introducer of many valuable varieties of nuts. He is believed to have been first to breed filberts by hybridization of species. Beginning in 1917, he sought to cross European varieties of *Corylus avellana* with the Rush hazel, *C. americana*. Being entirely unsuccessful for 2 years, he reversed the order in 1919 with immediately favorable results. By this method he developed the Bixby and Buchanan varieties, which have been named and introduced since his death.

In that paper Swayne told of a series of experiments begun by him in 1820 and continued for 3 years. During the first year he suspended catkins of the wild hazel (*Corylus avellana*) in the tops of two filbert trees having profuse pistillate blooms but a scarcity of staminate flowers. The trees had been owned by him for 14 years, during which time there had been practically no crops. That year, however, following the application of abundant pollen, the yield was "exactly 2 pounds." With this encouragement he checked the experiment the following year by first noting as before that the pistillate flowers were abundant but that there were practically no staminate flowers. He refrained from adding pollen and the crop that year was again a practical failure. The next year, when for the third time there were many pistillate flowers and few staminates, he made applications of pollen from the wild hazels to the stigmas of the garden trees. The crop was again very good, and soon after the harvest he reported the results of his 3 years' work.

So far as known, the next investigation of this nature occurred almost a century later when, in 1917, the late J. F. Jones (fig. 1), of Lancaster, Pa., sought to hybridize the European varieties of filbert with the Rush variety of American hazel, *Corylus americana* (fig. 2, *A*). He and many others had found the former not commercially



Corylus varieties that have been successfully used in eastern filbert breeding: *A*, Rush (*C. americana*), the pistillate parent mainly used; *B*, Barcelona (*C. avellana*); *C*, Rush × Barcelona, Buchanan variety; *D*, Du Chilly (*C. avellana*); *E*, Rush × Du Chilly; *F*, Italian Red (*C. avellana*); *G*, Rush × Italian Red, Bixby variety; *H*, White Aveline (*C. maxima*); *I*, Rush × White Aveline.

Figure 2.

hardy in the East, and the Rush was the best of the native hazels that came to his attention. For 2 years he applied Rush pollen to the pistillate flowers of several European varieties, with negative results. In 1919 Jones reversed the order and there was a good crop of nuts. These were planted during the following spring, and from that time until his death in January 1928, Jones was an active and enthusiastic filbert breeder. His hybrids came into bearing early, and by 1924 about 100 were in fruit. By the end of the next 3 years he had selected 12 to 15 for further observation and eliminated a considerable number. One that had been numbered 200 proved so promising that he was seriously considering its propagation and introduction to the public. This plant was the result of a cross between Rush and Italian Red. It has since been named Bixby (fig. 2, *G*) after the late Willard G. Bixby, of Baldwin, N. Y., a friend and coworker of Jones. Another plant, no. 92, greatly resembling Bixby, but shown by Jones' record to be a Rush × Barcelona cross, has been named Buchanan (fig. 2, *C*) and is being propagated for the nursery trade. Both Bixby and Buchanan are apparently of considerable promise for home planting in the East

Figure 3.—Felix Gillet (1835–1908), proprietor of Barren Hill Nurseries, which he established at Nevada City, Calif., in 1871. He was one of the most outstanding figures of his time in introducing carefully selected varieties of filbert. Persian walnut, and chestnut from Europe.

European Filberts in the Eastern United States

In the aggregate there has been a large amount of selection work with the filbert in this country during the past century or more. Plantings of European varieties and seedlings have been made frequently in various sections. Most of the better varieties and seedlings were introductions made during the eighties and nineties by the late Felix Gillet (fig. 3), a Frenchman who established a nursery at Nevada City, Calif., in 1871. A good many introductions have been made by others, so that altogether several hundred varieties and seedlings from Europe have been tried out in this country. The best of these have proved commercially profitable only in the Pacific Northwest. They have been successful in the East to a limited degree and as a rule only when grown in situations well protected from extremes of temperature, as by a large body of water, a building, a hill, or a group of trees.

Three known factors stand in the way of success with the European varieties of filbert in the East. The most important is a serious blight, *Cryptosporella anomala* (Pk.) Sacc., which causes little injury to the native species but spreads quickly and with fatal results to

European varieties planted in the vicinity. The likelihood of serious losses by this disease has decreased greatly during the last half century with the more or less general eradication of the native hazel plants on roadsides and fence rows, incident to clearing the land. However, the disease is still a grave menace whenever either European varieties or the new hybrids (*Corylus americana* × *avellana*) are planted near native species growing wild.

The second factor is lack of hardiness. Most European varieties of filberts are subject to winter injury, which may kill only the staminate flowers, or the pistillate ones, or both, or it may kill the tree tops, or even the tree trunks to the ground. As a rule, however, only the flowering parts are injured.

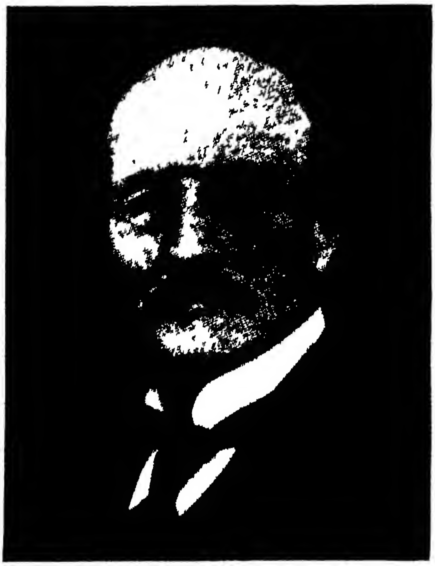


Figure 4.—A. A. Quarnberg (1849–1933), Vancouver, Wash., one of the leading figures in laying the foundation of both the filbert and Persian walnut industries in the Pacific Northwest. He was one of the first to plant and test most of the varieties now of leading importance in that part of the country.

The third factor is self-sterility. So far as known all varieties are largely, if not entirely, dependent upon other varieties for effective pollination. Until recent years most plantings in the East were made without regard to pollination requirements.

Some of the men who were most active in the introduction and early testing of varieties of filberts in the Pacific Northwest were A. A. Quarnberg (fig. 4), Vancouver, Wash.; Thomas Prince, Dundee, Oreg.; and George A. Dorris, Springfield, Oreg. Among those most recently active in the field of selecting and testing new varieties are Pearcy Bros., Salem, Oreg.; H. A. Henneman, Portland, Oreg.; A. M. Gray, Milwaukie, Oreg.; W. A. Schmidt, Corvallis, Oreg.; A. B. Scherf, Newberg, Oreg.; and D. Fitzgerald, Washougal, Wash. These men procured their trees mainly from Gillet, but to some extent they made direct importations. Among those in the East who have contributed most to filbert culture since the early eighties may be mentioned the United States Department of Agriculture; the New York State Agricultural Experiment Station at Geneva; A. S. Fuller, Ridgewood, N. J.; J. W. Kerr, Denton, Md.; Conrad Vollertsen, Rochester, N. Y.; Robert T. Morris, Stamford, Conn.; W. G. Bixby, Baldwin, N. Y.; and J. F. Jones, Lancaster, Pa. Vollertsen brought a number of varieties from Germany in 1912. Of these, Italian Red (fig. 2, *F*) is the only one now in special favor among eastern planters. Dr. Morris introduced a valuable seedling from Bohemia, which he later named Bonybush. The other men named in this group made their contributions by testing varieties in their respective localities.

Raw Material for Filbert Breeding

Most filbert varieties of either American or European production are without conspicuous merit. As previously noted, few are both hardy and fruitful except in specially favorable environment. Most filberts are of medium palatability and the nuts of many varieties are often imperfectly developed and the kernels thickly coated with coarse fiber. Some varieties are poor bearers, or the nuts may be too small or too thick-shelled to be acceptable on the market. Many are difficult to extract from the husks, and some produce only small quantities of pollen.

Some varieties are very good in quality and flavor. The nuts of some are of good size and thin-shelled. The kernels are often plump and bright-colored. The best nuts are entirely free from coarse covering over the kernel. However, some of the finest are too small for commercial use. White Aveline (fig. 2, *H*) is typical of the mixture of good and bad characteristics found in filberts. In quality of kernel it is one of the finest varieties known. It also has a remarkably thin shell; but, since it belongs to the species *Corylus maxima*, it has a long, tubular, tightly closed husk, which fails to open at maturity, and husking is difficult.

The variety with the greatest number of good points now grown in this country is Barcelona (fig. 2, *B*), which was introduced from Europe by Gillet probably during the seventies or early eighties. The tree is a vigorous grower and a good bearer; the nuts ripen early and within a short period and readily fall free of the husk. They are attractive in appearance and of large size. The shells are of medium thickness, and the kernels are usually plump, clean, quite sweet, of fine texture, and fairly rich. The nuts are roundish in form, although variably so. The kernels are not so clean or free from covering over the pellicle as some others, nor are they the best in flavor. Nevertheless, everything considered, commercial growers of the Willamette Valley, Oreg., have thus far found this to be their most profitable sort.

The second leading variety in the Pacific Northwest is Du Chilly (fig. 2, *D*), also an early European introduction made by Gillet. As compared with Barcelona it is moderately vigorous, not as productive, and less hardy. The nuts do not mature quite so early, and only a small proportion are naturally separated from the husks, although they are not difficult to husk. The nuts are oblong and flattened instead of being roundish. The shell is about as thick as that of Barcelona. The kernel is similar in plumpness and about equally free from fibrous covering. It is slightly sweeter and more palatable than Barcelona. Du Chilly nuts bring a somewhat higher price in the market, which largely, if not entirely, offsets the lighter fruiting of the variety. Both Du Chilly and Barcelona are less inclined to throw up suckers persistently about the base of the tree than are some others.

Daviana is the best known of the large varieties from Europe, which are notably thin-shelled. It is an excellent pollinizer for other varieties, but is itself a shy bearer, is very subject to injury by a bud mite, and frequently the kernels are not plump. From the standpoint of the breeder, its chief advantages are believed to be thinness of shell and its value as a pollinizer.

Nature of the Problems Involved

The problems involved in filbert breeding are relatively simple as compared with those of the chestnut, since there is already ample material. The area in the Pacific Northwest within which commercial filbert growing is centered is relatively small and has many full collections of varieties. In the East species and varieties now thought essential are represented in collections of the Bureau of Plant Industry, United States Department of Agriculture, near Washington, D. C., and of the New York State Agricultural Experiment Station at Geneva. Breeding by hybridization has made much headway at each place. Also a valuable collection of first-generation hybrids between Rush, one of the best-known native varieties of *Corylus americana*, and certain leading European sorts, mainly of *C. avellana*, is under observation at the J. F. Jones Nurseries, Lancaster, Pa.

Present Breeding Work and Future Possibilities

The most promising line of attack for the breeder in the East seems to be a continuation and expansion of breeding by hybridization, such as is already under way, rather than by making further selections from European varieties or the native species, both of which generally fall below the standards of American growers or consumers. Until superior hardy varieties can be developed, the best of the American varieties are likely to be used to a limited extent for home planting in zones beyond the climatic limits of safety for hybrids or European varieties.

In the Pacific Northwest the problem of the breeder is to develop more perfect varieties, chiefly from seedlings of *Corylus avellana*. The problem of hardiness is less acute than in the East. A desirable variety in the Northwest would be one that is resistant to fungus diseases and insect pests, a strong grower, either self-fertile, or a good pollinizer for other varieties, and a heavy annual bearer of choice nuts. The nuts should mature early and all at one time; they should separate naturally from the husks; they should be bright-colored, uniform in size, and probably oblong rather than rounded for greater appeal to the consumer. The shells should be thin enough to be broken easily, and the kernels should be plump, clean, bright, sweet, and of fine texture. In the appendix will be found a list of breeders engaged in work with the filbert, and of varieties considered promising for breeding work.

On the western coast filbert breeding is still largely carried on by mass selection. Out of the thousands of seedlings that are being grown and tested by private growers, the best finally come under critical observation when all but an extremely small percentage are rejected. Few varieties have yet come to light that meet the dual requirement of commercial crop production and pollination of other varieties. When breeding reaches the point of seeking greater hardiness in order to widen the western range of successful production, it is not improbable that the wild species, *Corylus californica*, of that region will be given a trial as one of the parents, in the same way that *C. americana* has been used successfully in the East. Thus far, pollen of neither of these native species has been found to function on the

pistillate flowers of European varieties, but as the eastern species has been useful as a pistillate parent, the same may prove true with the western one.

Filbert breeding, both by selection and by hybridization, is in progress at a number of points in the East. The United States Bureau of Plant Industry has made important contributions in its studies of varietal values not only in that part of the country but also in the Pacific Northwest. It has also made a number of important introductions of varieties from Europe. It is continuing its studies of the merit of European varieties both at the Arlington Experiment Farm, Arlington, Va., and at the United States Horticultural Station, Beltsville, Md. The work at the latter place is now largely confined to testing first-generation hybrids resulting from crosses made by its staff on the grounds of the late W. G. Bixby, Baldwin, N. Y. The pistillate parents used in making these crosses were Rush, Littlepage, and Winkler varieties of *Corylus americana* as well as a number of varieties of *C. avellana* and *C. maxima*. Among others used as pollen parents were *C. colurna*, the Turkish tree hazel, and *C. heterophylla* Fisch., from eastern Asia, sometimes called the "various-leaved hazel." Altogether, there are now at the Beltsville station about 2,000 hybrid plants of bearing age, transplanted from the nursery from 1932 to 1936. Several of those that have fruited appear highly promising for home use. Nuts of the first generation are a little small for sale in the unshelled condition.

Hybridization of filberts at the New York (State) Agricultural Experiment Station was begun in 1930. In 1933, 535 hybrid plants resulting from crosses made by Federal workers were transferred to Geneva from the Bixby grounds at Baldwin, N. Y. Some of these now in bearing are exceedingly promising. In addition to these plants there are 352 other plants at Geneva resulting from more recent crosses made by station workers. Climatic conditions at Geneva seem to be more favorable for varieties of *Corylus avellana* than at either of the Federal stations, but partial or complete crop failures are not infrequent even there.

The Virginia Agricultural Experiment Station at Blacksburg began selective breeding from Kentish Cob seedlings in 1921. The purpose has been to develop hardy varieties of merit for use in that State. One seedling has been selected as worthy of further observation.

The Minnesota Agricultural Experiment Station at University Farm, St. Paul, is breeding by selection from native plants of *Corylus americana* for the purpose of developing hardy varieties of value in that State for home planting. About 200 plants have been brought to fruiting and discarded. Nine hundred more are now under observation, of which some appear to have considerable promise.

Working privately, S. H. Graham, Ithaca, N. Y., is doing considerable filbert breeding, mainly by selection. However, he has brought into fruit a number of second-generation hybrids of the crosses made by the late J. F. Jones, Lancaster, Pa. From these he has made one or two selections of considerable promise.

E. M. Ten Eyck, South Plainfield, N. J., has had for many years a number of *Corylus avellana* seedlings grown from nuts bought on the market. These have been injured very little by winter temperatures,

have borne well, and the nuts have been quite satisfactory for home use. C. P. Close and J. J. T. Graham, of the United States Department of Agriculture, have both grown for many years a considerable number of seedlings of *C. avellana* from which it now seems possible to make selections of value for home planting. The trees of Close are at his home in College Park, Md., and those of Graham at Glenn Dale, Md.

The J. F. Jones Nursery, Lancaster, Pa., is now fruiting and continuing under test about 50 first-generation hybrids from crosses made by Jones. As already noted, two of these have been given variety names and are being propagated commercially. While it is improbable that further selections will be made for production varieties, it is possible that some of this collection will be found useful as pollinizers.

There is a large 24-year-old Barcelona tree on the premises of C. A. Reed, Takoma Park, Md., which bore a full crop for the first time in 1936, although it has bloomed freely with great regularity. Apparently it was effectively pollinated in the spring of 1936 by pollen from first-generation Rush × Barcelona hybrids nearby. If further investigation should prove that a Rush × Barcelona hybrid will effectively pollinate Barcelona, which is both self-sterile and sterile to Rush and to all other varieties of *Corylus americana*, the result will be extremely interesting as well as significant. If such hybrids can be used as pollinizers for Barcelona and other European varieties whose staminate flowers are easily killed by winter temperatures, the successful cultural range of such varieties might be considerably widened.

Progress already made in the improvement of filbert varieties by hybridization indicates great future possibilities for this kind of work. It should be possible within a reasonable period to develop superior varieties for commercial growing in the Pacific Northwest with which to meet the requirements of American markets now largely supplied by imports. Eastern varieties of high merit should be developed for home planting over much of the region from lower New England and the Great Lakes on the north to perhaps the Potomac and Arkansas Rivers on the south. No doubt much of Wisconsin, southern Minnesota, South Dakota, and Nebraska might also be included.

THE HICKORY GROUP

THE hickories form an important group of trees valuable for the production of both nuts and timber. With the exception of a single species, *Hicoria cathayensis* Sarg., from southeastern China, the entire genus is strictly American. The hickory range extends from the Provinces of Quebec and Ontario in Canada across the eastern and central United States into northern Mexico. Fifteen species are described by Sargent in the Manual of the Trees of North America. Of these only three or four produce nuts of particular value, although the nuts of certain others are edible in varying degrees.

From the standpoint of value of nuts the pecan, *Hicoria pecan* (Marsh.) Britton, is the most important member of the group. In crop value it rivals the Persian (English) walnut of the western coast. The tree is one of the largest east of the Rocky Mountains. Broadly

speaking, the natural and cultivated range of the pecan covers the Cotton Belt and lower elevations northward in the Mississippi Valley into Indiana, Illinois, Iowa, and southeastern Kansas.

The pecan tree is valuable in ornamental planting wherever climatic and soil conditions are favorable. It sometimes succeeds as far north as Connecticut, but nut production is unimportant north of the District of Columbia or the latitude of Terre Haute, Ind.

Other hickories offering inducement to breeders include the shagbark, *Hicoria ovata* (Mill.) Britton, the shellbark, *H. laciniosa* (Michx. f.) Sarg., and a number of other species of less importance, as well as various hybrid forms that occur with considerable frequency in nature. The shagbark is much the most valuable nut producer. Nuts of the shellbark, while large and alluring, are often poorly filled.

Breeding to improve hickories of any species has thus far largely been confined to selective methods. By such means a very considerable number of varieties of both pecan and others have been brought to light. Breeding by hybridization has been under way with the pecan for many years, but so far without the introduction of many varieties. This form of breeding has not yet been undertaken in earnest with other hickories.

Pecan

According to dates given by Taylor (*38*), pecan selection is known to have begun as early as 1846 or 1847, when scions of a variety later named Centennial were successfully grafted by a Louisiana slave named Antoine. The next variety known to have been grafted was Van Deman, in 1877, although it was not permanently named until 15 years later. The Rome variety was first propagated in 1882, Hollis in 1884, Frotscher in 1885, Stuart in 1886, and Pabst in 1890. The first pecan nursery was that of William Nelson, New Orleans, La., who began selling seedlings in 1874 and grafted trees in 1879. The period of greatest activity in the introduction of new varieties was probably between 1905 and 1925. During that time practically every important pecan center of the entire South introduced its favorite varieties of local origin.

The first carlot shipment of pecan nuts of named varieties, carefully graded according to definite standards of size and quality, is believed to have been made in 1917 by J. M. Patterson, president of the Georgia Papershell Pecan Growers' Association, Putney, Ga. By 1920 there was a great multitude of varieties in bearing, and nuts of the same size and general character, whether from seedling trees or named varieties, brought about the same price. This caused the selling agencies to begin marketing a large portion of the crop by brand instead of by variety as had been done until that time. Now, with the exception of a few varieties, such as Schley and Stuart, most of the pecan crop, no matter whether from cultivated or wild trees, is graded according to size, form, appearance, and to some extent thinness of shell and general merit. High uniformity, possible only when varieties are sold separately, has largely disappeared, at least for the time being.

The loss of varietal status, insofar as selling pecans is concerned, has been partially due to the failure of a good many varieties to meet the requirements of successful production and marketing, and of any

varieties to become outstanding. Light bearing, uncertain filling, variability in size of nuts from year to year, even from the same trees, together with susceptibility to insect pests and fungus diseases, have had much to do with a situation that has practically compelled the blending of the nuts of the different varieties together instead of selling them separately. A process of readjustment is now taking place throughout the entire field of production and will probably continue until a majority of present varieties have been superseded by new kinds better suited to the requirements of the orchard and the market. Future plantings will doubtless be established with superior varieties now unknown, and with greater consideration of environmental and cultural requirements.

Figure 5.—E. E. Risien, San Saba, Tex., a pioneer in propagation and varietal improvement of the pecan by selection and hybridization. A majority of the most popular varieties of Texas are among his productions.

Past Breeding Work With Pecans

Apparently the first breeder of pecans by hybridization was Forkert (*13*), of Ocean Springs, Miss., who began this work in 1903. He was followed 1 year later by Risien (*29*), of San Saba, Tex. Both men were of foreign birth, Forkert having been born in Germany and Risien in England. They spent much time in searching for the best varieties obtainable by selection from seedlings before undertaking the work of hybridization. Forkert found no chance seedlings that he thought worthy of introduction, but Risien introduced several varieties selected from wild seedlings.

Forkert's first introduction, Dependable, was the result of a Jewett×Success cross. This proved disappointing and has since been practically abandoned. Admirable, a Russell×Success hybrid, also was a disappointment insofar as being an improvement over existing varieties was concerned. His one apparently meritorious introduction is Desirable, a variety of unknown parentage. It was not widely disseminated previous to his death in 1928, and would doubtless have been lost had it not been for scions that he sent to the United States Pecan Field Station near Albany, Ga., in 1925. From this stock the variety has been widely disseminated for test planting.

The work of Risien (fig. 5) was in a semiarid region at high altitude in western Texas. He seems to have been the first in the South to conduct a systematic survey of wild pecans for seedlings worthy of propagation as new varieties. About 1882 (*30*) he discovered the parent tree of the variety that he later named San Saba. He was probably the first to plant nuts from a selected tree in orchard form

for the purpose of growing seedlings from which to make selections. A great many persons planted seedling trees for nut production during that early period because grafted trees were unavailable, and from such trees many good selections were made later. Risien planted chiefly for the purpose of originating valuable varieties, and in this he was successful.

Risien independently mastered the art of propagating pecan trees during the early nineties, and while he was a half century behind Antoine in this work, so far as is known he was the first propagator in Texas, and so far as he knew he was the pioneer in the field. He was the first in the South to top-work large pecan trees. In addition to San Saba, he introduced Attwater, Kincaid, and Sloan as selections from wild seedlings. Among the selections from his orchard of 1,000 San Saba seedlings are Colorado, Jersey, Libertybond, Onliwon, San Saba Improved, Sovereign (Texas Prolific), Squirrels Delight, Supreme, and Western (Western Schley). Among varieties from definite crosses are Banquet (Sovereign×Attwater), Commonwealth (Longfellow×Sovereign), Kincaid Improved (Onliwon×Kincaid), Sloan Improved (San Saba×Sloan), and Venus (San Saba×Attwater). A recent introduction is Garner (John Garner), an open-pollinated seedling of San Saba Improved.

Another Texan who has contributed much to the pecan industry, not only in his native State but also in the entire South, is J. H. Burkett, of Clyde, Tex., for many years chief of the division of edible nuts in the State department of agriculture at Austin, and author of several bulletins on pecan culture. Burkett was the discoverer and introducer of the valuable Burkett variety, which has a large, round nut with very thin shell and excellent kernel characteristics. It has long been a favorite among planters from western Texas to the Pacific coast. It has several features that should make it desirable for use in breeding work.

Other planters in many States, covering practically the entire South, established seedling pecan orchards having from a few hundred up to several thousand trees. One such orchard, planted in 1897 by James (*17*), of Mound, La., later became the source of such important varieties as Carman, James, and Moneymaker. During approximately 30 years, beginning in 1880, seedling orchards and dooryard trees on the Gulf coast of Mississippi, especially in the vicinity of Ocean Springs and Pascagoula, became fruitful sources of new varieties. It was then that Alley, Delmas, Pabst, Russell, Schley, Stuart, Success, and many others less prominent were introduced from that section. Among persons most active in the introduction of these varieties were Theodore Bechtel, C. E. Pabst, and W. R. Stuart, of Ocean Springs, and A. G. Delmas, I. P. Delmas, and F. H. Lewis, of Pascagoula.

In northwestern Florida during the nineties, seedlings grown from nuts of trees owned by Arthur Brown, Bagdad, Fla., had an important part in giving rise to varieties in that region. An orchard planted with such stock in 1886 by J. B. Curtis at Orange Heights, Fla., became the source of the Curtis variety in 1896, and of Hume, Kennedy, and Randall somewhat later. Many other Florida varieties, less well known, are believed also to have originated as seedlings of the Arthur Brown stock.

Probably the first large-scale breeding of pecans by hybridization was begun by the United States Bureau of Plant Industry in 1915 in the orchard of C. E. Pabst, Ocean Springs, Miss. Hundreds of crosses were made that year and the next, and the resulting nuts were planted on the grounds of Pabst. However, with the entrance of the United States into the World War the work was discontinued and the young trees were neglected. Pabst died in 1919, and with the change in ownership of the property the entire lot was lost.

This work was resumed in 1920 in the orchard of B. W. Stone, Thomasville, Ga., and continued for several years. The first nuts were planted on the grounds of the Georgia Experiment Station, Experiment, Ga. Of these, a Schley × Moneymaker hybrid is now believed to have considerable promise. In 1922 the United States Pecan Field Station at Philema, Ga., was established, and several thousand young hybrid trees were soon developed. In 1930 the youngest trees were transferred to the United States Pecan Field Station at Robson, La. A considerable number of trees at the former station have been in bearing for several years and are now being observed closely with regard to bearing habits, disease resistance, and merits of nuts. Some of these hybrids are highly promising but require considerable further observation.

In the North, where the native pecans are mostly small and difficult to crack but otherwise much like those of the Southeast, the first recorded steps toward selecting varieties began during the early nineties, when the Department of Agriculture received nuts from Illinois, selected mainly because of their superior size. One of the first trees to attact attention in this way belonged to H. G. Hodge, York, Ill. During the next few years this variety came to be known as Hodge's Favorite or Illinois Mammoth, and many nuts from the original tree were sold for seed purposes. It was accorded varietal recognition by Taylor (*38*) in 1908, who called it Hodge.

The second northern pecan variety to be recognized appears to have been Major, discovered by W. N. Roper, Petersburg, Va., about 1907. His attention was attracted to the superiority of certain nuts in a mixed shipment that he procured for seed purposes from a merchant in southern Indiana. By persistent efforts Roper traced the nuts to the parent tree near Green River in northern Kentucky, some 15 miles southeast of Evansville, Ind.

The next step toward bringing out new northern varieties seems to have been made in 1908, when a pecan contest was held at Mount Vernon, Ind., under the direction of the Purdue University Agricultural Experiment Station. It was then that Warrick, now practically obsolete, was brought to light.

During the period of 1910 to 1915, Simpson Bros., Mason J. Niblack, and W. C. Reed, Vincennes, Ind.; J. F. Wilkinson, Rockport, Ind.; and Thomas P. Littlepage, a native of the Rockport region but then a resident of Washington, D. C., spent much time, labor, and money in searching for other worthy varieties. It was during this period that Busseron, Butterick, Greenriver, Indiana, Kentucky, and Posey were recognized and introduced. From then until quite recent years very few other northern sorts have come to notice. However, beginning

in 1933 and continuing annually since, a pecan contest has been held in New Haven, Ill., under the direction of H. C. Neville, formerly farm adviser of Gallatin County. As a result of these contests several highly promising varieties have come to light, but they have not yet been offered by nurserymen. In 1934 a nut contest conducted by the Northern Nut Growers' Association brought out several apparently desirable new varieties, which ought not to be lost. Present-day breeders of pecans are listed in the appendix.

Problems in Pecan Breeding

The known defects of present varieties of pecan are many, regardless of the reputation the species justly enjoys of being one of the finest of table nuts. In the orchard many varieties are seriously susceptible to attack by insect pests and diseases of various kinds. Other defects include shy bearing; late ripening; weak crotches, which split badly; wood that breaks under the weight of nuts, especially late in summer during storms; poor shelling characteristics; failure to fill well; lack of good flavor; and a tendency of the nuts to germinate before dropping from the trees, when dry summer weather is followed by wet periods late in the growing season.

Pecans reach the consumer in two forms, shelled and unshelled. The kernels are known in the trade as shelled nuts, and by far the greater portion of the crop is marketed in this form. Nuts of small and medium sizes from either the forests or orchards are sold as "halves" or "pieces." Pecan halves are used as salted and roasted nuts and in capping such products as cakes, breads, and candies. Pieces are used as an ingredient in pastry, ice cream, and confections. For capping, the smaller the halves the better, since this means a larger number per pound. Seven hundred per pound is usually the minimum required.

When the cultivated crop is of bumper proportions or offgrade for any reason, so that prices are inclined to drop, many of the nuts are diverted from the unshelled to the shelled market. Prices for cultivated varieties, once 10 to 50 times as great as for the medium to small nuts from the forest, are now only 2 to 5 times as great. The best prices now being received by growers for cultivated pecans is about one-fifth of what it was two decades or more ago when the great majority of the present varieties were discovered and introduced.

In the present economic status of the pecan industry the most profitable varieties are those that are the most productive largely without regard to other qualities. Fruitfulness, therefore, is the characteristic sought above all others, often to the exclusion of other important factors, particularly quality and flavor.

Some of the choicest pecan varieties, from the standpoint of the nuts alone, are no longer being planted because of extreme susceptibility to fungus diseases, failure to bear well, or deficiencies of kernel. Often these weaknesses are aggravated by unfavorable environmental conditions such as severity of climate, poverty of soil, or too close planting. For these reasons it is impossible to attribute the failure of any given variety to any single factor or to any particular combination of factors. It is equally impossible at this time to predict with certainty the commercial requirements for varieties in the future.

However, it seems to be a reasonable assumption that pecans will be marketed more and more in the shelled condition, and varieties must be developed with this requirement in view. Present varieties can, in many cases, be made to give more satisfactory results by improving cultural practices according to knowledge now available.

Desirable combinations of nut characters are to be found in a good many varieties. In the nursery and orchard such points as ease of propagation, rapid growth, precocity, productiveness, and resistance to disease are all to be found, distributed variously among the different varieties but not in perfect combination in any. For example, well-grown nuts of the Schley variety have good size, handsome appearance, suitable form for shelling by hand or machine, very thin shells, good shelling quality, and superior kernel characteristics. The variety is easy to propagate, is a rapid grower, and forms a symmetrical tree. It begins bearing at a relatively early age and normally is fairly productive. However, the susceptibility of Schley to scab makes it undesirable for commercial orchard use. Another example is Moneymaker, which is easy to propagate, a rapid grower, precocious, prolific, and early in ripening. On the other hand, the nuts are roundish in form, variable in size, not especially thin-shelled, not easy to shell by hand, and medium in quality and flavor of kernel. In appearance the nuts are only moderately attractive, and the tree is so susceptible to certain leaf diseases that it is no longer in favor with leading growers.

Three well-known eastern pecan varieties having outstanding points, which should be useful in breeding, are Curtis, Moore, and Stuart. Curtis nuts are among the best of any variety to eat out of hand. They are a little small but quite thin-shelled and easily cracked, and the kernels are very fine, being plump, rich in quality, and unusually sweet. Moore is one of the most prolific bearers and the nuts ripen with the earliest. Stuart is probably the most dependable variety in the Southeast. While it is not a heavy bearer, in most localities it performs consistently and the nuts are large, attractive in appearance, and uniform in size.

Among varieties of the western group, Burkett, Halbert, and Sovereign are well known and probably as useful for breeding purposes as any. All begin bearing at an early age and increase in productivity rapidly. The shells of Burkett and Halbert are remarkably thin. The kernels of all are plump, bright-colored, and distinctly superior to those of most other varieties.

The problem of improving pecan varieties by breeding is greatly affected by the uncertainty as to future market requirements. With few exceptions past efforts have been to develop varieties for the unshelled market. For this purpose, large size has been one of the principal assets. Two small varieties, the Candy, by Theodore Bechtel, of Ocean Springs, Miss., and the Reuss, by G. B. Reuss, of Hohen Solms, La., were introduced at about the same time many years ago for sale in the shelled trade. These nuts were unusually thin-shelled and of excellent shelling and kernel qualities. The parent trees in both cases were heavy bearers, but neither variety met with favor on the part of nurserymen or planters on account of the small size of the nuts. However, the nuts of neither were small enough to meet the present market requirement of more than 700 halves to the pound,

and it is an open question as to whether either would be of particular value in breeding to develop smallness in size. Probably the only varieties that can meet this requirement are a few recently brought to attention in some of the Northern States but not yet well tested.

Growers as a class prefer not to produce pecans of small size. In fact it is doubtful whether it would be profitable for them to do so at the present time. The question is to what extent, if any, it would pay to raise pecans exclusively for the shelled market. The demand in that direction is usually well supplied with pecans from the forests or those from the cultivated orchards that might be classed as imperfect or surplus pecans. It may be that, with the exception of the peanut, which strictly speaking is not a true nut, none of the American-grown nuts can compete on a price basis in the retail market for shelled nuts with certain foreign species that are produced at much lower labor costs. It is certain, however, that very large pecans no longer sell readily to discriminating consumers. It is also true that greater portions of the crops from orchard trees are steadily finding their way into the shelled market. It would be very desirable, if possible, to determine the probable future market requirements as to size. In the absence of a basis for an accurate prediction as to what the future may bring forth in this direction, it will probably be well to follow the present trend, which is definitely toward nuts of medium size. The largest nuts from these crops can be separated out by sizing machines and sold in the increasingly more limited market willing to pay a premium for such sizes.

The best pecan varieties lack certain characteristics necessary to make them ideal New varieties with all the features of an ideal nut are not to be expected until a planned program of breeding to accomplish certain definite ends is carried out Such a program would involve the growing of a large number of second-generation hybrids from the best breeding stock. In this way alone will it be possible to develop material from which to select varieties resistant to disease and superior in other characteristics. Cytological analyses of varieties may be expected to yield information as to their value as breeding stock and to throw light on problems of pollen viability and sterility.

Present Breeding Work and its Aims

Pecan breeding as it has long been carried on by the Bureau of Plant Industry has for its objectives improvement along seven distinct lines. These are (1) hardiness, (2) disease resistance, (3) fruitfulness, (4) size of nut, (5) shell thinness, (6) shelling quality, and (7) kernel quality. The purpose is to develop good varieties that can be grown with profit in each of the three distinct natural pecan districts, southeastern, southwestern, and northern. The southeastern district extends from the South Atlantic seacoast west to central Texas. The southwestern district includes localities wherever the pecan succeeds from Fort Worth, Tex., west to Arizona and southern California. The northern district includes all localities suitable for pecan growing in the Mississippi Valley north of the latitude of Memphis, Tenn., and in the Coastal Plain or lower Piedmont regions in Virginia and northward.

No great amount of pecan breeding has yet been undertaken by State experiment stations. In cooperation with the Bureau of Plant Industry, the Georgia Experiment Station grew to fruiting several hundred seedling trees resulting from crosses made by Bureau workers at Thomasville, Ga. From these the station workers selected for further observation one designated as A–93, a Schley × Moneymaker hybrid. This is a strong-growing, fruitful tree producing nuts of considerable excellence.

The North Carolina Agricultural Experiment Station began breeding pecans at Willard, N. C., in 1912. From a large number of seedlings of named varieties station workers have selected a Schley seedling, RT–6–4, as being of much promise. The New Mexico Agricultural Experiment Station at State College, N. Mex., has made one selection from seedlings of named varieties. This is designated as College No. 1. It grew from a Sovereign nut that had been open-pollinated.

A certain amount of pecan breeding has been started in two foreign countries. The Department of Agriculture of New South Wales is doing preliminary breeding at the Breeding Station, Grafton Experimental Farms, Sydney, Australia. Selective breeding is under way in Mexico under the direction of the Secretariat of Agriculture, Department of Stations and Experimental Fields, Mexico, D. F.

Three different sets of pecan varieties are required to meet environmental conditions in the respective American regions. Greater hardiness is being sought in order that varieties may be used for planting north of the present limits and to safeguard more southern plantings against extremes of cold. Resistance to disease is one of the most vital points for the success of any variety. Many otherwise good varieties have had to be abandoned because of their susceptibility to fungus diseases. No factor is more important than that of productiveness. It makes little difference how worthy a variety may be in other respects—if it does not bear well it must be replaced sooner or later. By good nut size is meant medium rather than large. Overlarge nuts are objectionable because of the tendency to develop imperfect kernels. Pecans that will average 60 to 70 to the pound are most desired in the unshelled market. Thinness of shell and ease of shelling are also being sought after, as without these characters pecans in the shell are unlikely to compete successfully with nuts of other kinds that can easily be shelled in the hands or that are sold only in the shelled condition. Varieties of pecan of probable value for breeding are listed in the appendix.

Hickories Other Than Pecans

Selections from species of hickory other than pecan have resulted in the naming of a large number of varieties. Relatively few have been propagated by nurserymen and none has been planted in commercial orchards. A considerable number have been top-worked on trees of bearing age, and a few, grown as nursery trees, have been established in small test orchards.

Improvement of the hickories by selection was strongly urged as early as 1855 in an article by S. Hale, Keene, N. H., in The Magazine of Horticulture, in March of that year. The earliest record of hickory

selection appears even before that, as the "Perkiomen Shellbark" was brought to light in October 1853, when Abraham Wismer, of Perkiomen Township, Montgomery County, Pa., exhibited nuts of this seedling as "a large variety with thin shell and kernel of best quality." There is no record that this "variety" was ever propagated by budding or grafting, and it may be assumed that it is now lost.

The next northern hickory to receive varietal recognition seems to have been the so-called Hales Papershell, a thin-shelled variety of shagbark discovered by Henry Hales, of Ridgewood, N. J., first recorded by A. S. Fuller in 1870 and first propagated by J. R. Trumpy, of Parsons & Son, nurserymen of Flushing, N. Y., about 1880. This variety was propagated to a limited extent and widely disseminated throughout the East over a period of many years. It is now practically obsolete.

Figure 6.—Robert Tuttle Morris, Stamford, Conn., who has contributed much to the published knowledge of species and varieties of native nuts in the Northeastern States. In 1905, 1906, and 1907 he conducted annual contests for the best walnuts and hickories. He became charter president of the Northern Nut Growers' Association, founded in 1910. He has written many articles and one book pertaining to various phases of nut culture, especially propagation.

The next varieties to receive recognition grew from nuts planted in 1885 by J. W. Kerr, Denton, Md. Kerr sent away for "shellbark" seed nuts, which he planted along the roadways of his farm. From the resulting trees he selected a number of seedlings to which he gave varietal names. He grafted some of these on his home grounds, but so far as known none was established elsewhere and none is now believed to be in existence.

Varietal names were used for hickories in the annual report for 1891 of H. E. Van Deman, pomologist of the United States Department of Agriculture. He described Leaming, from Rush G. Leaming, Sedalia, Mo.; Milford, from O. C. Cook, Milford, Mass.; and Shimar, from Samuel C. Moon, Morrisville, Pa. In 1892 A. J. Coe, Meriden, Conn., offered a prize for the best hickory that might be submitted to the Connecticut Agricultural Society. The prize went to Whitney Elliot, of North Haven, Conn., for a variety named Elliot in his honor.

To Robert T. Morris (fig. 6), formerly a leading surgeon of New York, N. Y., but now retired and living at Stamford, Conn., belongs credit for beginning a movement in 1905 by which the majority of the varieties of hickory now known have been brought to notice. In that year he inaugurated a series of northern nut contests in which

cash prizes were given for the best nuts from seedling trees. These contests were continued for 3 years, then dropped. They were resumed in 1911 by the Northern Nut Growers' Association, a society founded in 1910 by W. C. Deming, then a physician of New York but now living at Litchfield, Conn. Dr. Morris was its charter president. The association has held many nut contests, the last in 1934.

During recent years other similar contests have been held. In 1926, under the guidance of J. Russell Smith, professor of economic geography, Columbia University, New York, N. Y., a contest for hickory varieties was held by the Philadelphia Society for Agriculture. A contest for northern nuts, including hickories and other species, was held in Michigan in 1929, under the guidance of the experiment station at East Lansing, and two excellent varieties of shagbark were brought out, Mann and Miller. These appear to be as promising as any yet discovered. The ownership of the parent trees has since changed hands one or more times, but both varieties have been successfully established by various persons, including G. A. Zimmerman, Harrisburg, Pa.

A similar contest for hickories was held in Ohio in 1933, and one for walnuts in the following year. New York held a general contest for nuts in 1934. The Ohio contests were sponsored jointly by the experiment station at Wooster and two members of the Northern Nut Growers' Association, C. F. Walker, of Cleveland Heights, and Homer L. Jacobs, of Kent, Ohio. The New York contest was directed by the State Experiment Station at Geneva, Cornell University at Ithaca, and S. H. Graham, Ithaca, a prominent member of the Northern Nut Growers' Association.

Following the discovery of the Perkiomen shellbark, previously mentioned, the shellbark seems to have received little attention until about 1915, when J. F. Jones, Lancaster, Pa., selected, named, and began propagating the Stanley shellbark from near Carthage, Ind. Other shellbarks, probably more desirable, have come to light during recent years. Along with the shagbark and the shellbark, a number of other hickories, such as mockernut, *Hicoria alba* (L.) Britton, and sweet pignut, *H. ovalis* (Wang.) Ashe, have been included in the search for varieties of merit. The mockernut is a handsome tree with dense, dark green, fragrant foliage, trunk bark without scales, and nuts having thick hulls, very hard shells, and small but sweet kernels. The sweet pignut also has handsome foliage and smooth bark. The hulls are thin, the shells moderately so, and the kernels often nearly as rich and sweet as shagbark. Neither species is as commonly associated with rich bottom lands as are the shagbark and the shellbark.

Few varieties of sweet pignut have been recognized or propagated. Probably the first and one of the very few introduced was Brackett, discovered in 1890 by G. B. Brackett, then of Denmark, Iowa. On the basis of nut characteristics alone a number of varieties of mockernut and other hickory species and types have been named, but very few of these are especially promising and in a majority of cases considerable uncertainty exists as to the identity of the reputed species.

Many natural hybrids between *Hicoria* species have been given varietal names and propagated to some extent. In many cases the

parentage on both sides is reasonably certain, but in others it is a matter of conjecture. Some of the earliest hybrids to become known were apparently pecan × shellbark crosses, including McCallister from Indiana, Nussbaumer from Illinois, and Rockville from Missouri. The Burton variety from near Owensboro, Ky., is supposed to be a pecan × shagbark cross. All of these were first grafted during the early nineties, or possibly earlier.

The natural type of hybrid of special value occurring most frequently among the hickories is probably shagbark × shellbark, one of the best varieties of which is Weiker, discovered in Lancaster County, Pa., by J. G. Rush, of West Willow, and first propagated in 1903 by J. F. Jones, then of Monticello, Fla. Other supposed hybrids are apparently crosses between pecan and bitternut, shagbark and bitternut, and pecan and mockernut.

Problems and Possibilities in Hickory Breeding

Hickory nuts have never met with the popular favor accorded pecans and black walnuts. In the shell they bring too low prices to justify shipment over long distances or extensive handling. Sale in the shelled condition is largely limited to small lots in local markets. Before nuts of the slow-growing hickory species can be expected to become popular enough with consumers to justify the planting of extensive orchards, irrespective of time or cost involved in bringing the trees into full bearing, varieties must be found or developed that can be shelled easily. Until this is done hickory nuts in the shell will probably continue to compete poorly with pecans, almonds, chestnuts, peanuts, and many of the Persian walnuts, most of which can be shelled easily without mechanical aid. All known varieties of pure species, and with few exceptions all of the hybrids, have shells either too thick or too hard to be cracked readily in the hands, though the shells of many may be readily broken open with a light tap of a hammer or by the use of some of the hand-power devices now on the market. The shells of many varieties split open when the nuts are hit on an edge with a hammer in such way as to release one half kernel perfectly while the middle partition holds the other half practically as securely as before the nut was broken open. A few varieties of shagbark have been found with shells of such thinness that breaking in the hands is not difficult, but in all such nuts that have been examined by the writers the cleavage has not been good. Instead of cracking along definite lines, the shells have merely mashed at the points where pressure was applied with another nut. With the exception of the pecan × hickory hybrids and pure pecans, which are usually oblong, all nuts of hickory varieties have been generally roundish in form and therefore quite unsuited for shelling in automatically fed machines.

The parent trees of some of the varieties are known to be heavy bearers during favorable years, and top-worked trees have come into bearing relatively soon, that is, in about the same time as is required for apples. The kernels of some are plump, bright-colored, sweet, and palatable. To many persons, especially to those who knew good shagbarks and shellbarks in childhood, no other nuts taste so good.

However, it is too early in the growing of these hickories to know how well any of them will be received by consumers, even when prepared in convenient and attractive form.

The problem of breeding other hickories, as in the case of the pecan, is difficult because of uncertainty as to what characteristics are likely to meet market requirements best. However, it may be assumed safely that the requirements for these hickories will not be very unlike those of the pecan and other nuts that are popular in the shell. In at least one respect other hickories should have an important advantage over the pecan. With the latter, seedling nuts of good size, good form for shelling, thin shells, and general excellence are not uncommon in the wild product. If such nuts exist among other hickories they have not yet been brought to light, in spite of many searches that have been made. When superior varieties of hickory are developed by breeding, as seems well within the realm of probability, they will have no competition with nuts of the same types, either wild or imported.

A small amount of breeding of other hickories by hybridization has been undertaken by the Bureau of Plant Industry. The objectives are much the same as for pecans. However, hardiness is more important than with the pecan because there is greater demand for varieties that can be grown successfully beyond the northern limits to which the various species are naturally adapted. This demand is from home owners who at present are unable to grow nuts of any kind for family use.

Nature has already laid much of the foundation for the hybridization program with hickories. It has produced many interesting hybrid forms, of which some may have considerable horticultural value. The majority of the first-generation hybrids are of little or no value except for novelty planting or further breeding. Very few second-generation hybrid populations have been grown, and until facilities are available for growing and studying large numbers of such progenies, progress will be slow in the selection of new and valuable types.

The natural hybrids are suggestive of what may be expected from crosses between certain species. For example, thinness of shell, and to a varying degree astringency, seem to be dominant in all bitternut (*Hicoria cordiformis* (Wang.) Britton) hybrids, and elongation of nut seems dominant in pecan × shellbark hybrids. Also, large size and uncertain or poor filling appear to be characteristic of hybrids between the pecan and either the shagbark or the shellbark.

By systematic breeding it should be possible to extend the range of the shagbark and other good hickories both north and south of present limits. A new form having the thinness of shell, the easy shelling character, and the rich quality of the pecan, the whiteness of shell of the shagbark, and the flavor of either pecan or shagbark, would be a great benefit to the nut industry. Such a nut is needed by orchardists, small home owners, and consumers.

In the appendix are given the names of breeders interested in improvement of the hickory and a list of varieties of probable value for breeding.

WALNUTS

Black Walnut

Five species of black walnut occur naturally in this country. Four of these are from the far West and Southwest and one from Texas. Of the former, two are from California, one from Arizona and New Mexico and one from New Mexico, Texas, and Oklahoma. The two California species are known as the Hinds or northern California walnut, *Juglans hindsii* Jepson, and the southern California walnut, *J. californica* S. Wats. The former grows to be a fairly large tree, now more commonly seen along roadsides and about residence grounds, where it has been planted for shade and ornamental effect, than in forests and fields. Nursery seedlings of this species are the stocks chiefly used on which to graft varieties of the Persian walnut.

The southern California walnut is a smaller growing and less valuable tree. It varies greatly in habit, depending upon its environment. Being drought-resistant, it often occurs in dry, gravelly, or unfriendly soils where other species of walnut would certainly fail entirely. Under such conditions it develops as a true shrub only 5 to 10 feet in height instead of as a standard tree. When conditions are more favorable it grows rapidly and becomes a fairly good-sized tree. It differs from the Hinds walnut in lacking a central leader, as its branches spread out in more or less vase shape. It is not planted to any great extent.

The two walnut species native in the Southwest are much alike and nowhere of great value. One is *Juglans major* (Torr.) Heller, from Arizona and southern New Mexico. This sometimes attains a height of 50 feet and a trunk diameter of from 3 to 4 feet, although ordinarily it is a small tree. The other species is *J. rupestris* Engelm., from parts of New Mexico, Texas, and Oklahoma. This is a shrubby tree rarely attaining a height of 30 feet. The nuts are the smallest of any American walnut. Generally speaking, all of these western and southwestern walnuts are of little value for either timber or nut production. They should be useful, however, in breeding hybrid strains for that part of the country.

The eastern black walnut, *Juglans nigra* L., is the most important native walnut of this country in both timber and nut values as well as in extent of native and adapted range. No other American timber tree equals it in value for such special uses as cabinetmaking, interior finishing, and the manufacture of many articles, particularly gunstocks. Few other tree species are so widely distributed over the entire United States. It is grown to some extent in practically every State in the Union. Under the most favorable conditions it sometimes attains a height of 100 to 150 feet and a trunk diameter of more than 6 feet. The nuts are variable in size, form, thickness of shell, and shelling quality and also in character and flavor of kernel. The kernels of this species are favorites with manufacturers of confections and baked goods on account of the extent to which the pleasing flavor is retained in the cooking processes. So far as known, the eastern species is the only black walnut thus far used in breeding.

The history of breeding the eastern black walnut closely parallels that of the northern hickories. It has been limited chiefly to the selection of varieties from wild trees, the propagation and testing of

many of these by amateurs, and the commercial planting of a few. The Thomas variety from Montgomery County, Pa., discovered, named, and first propagated about 1880 by J. W. Thomas & Sons, nurserymen, of King of Prussia, Pa., appears to have been the first to attain varietal status. It has since been widely disseminated and is still the general favorite with most planters. Its seedlings are notable because of their vigor and rapid rate of growth. Six varieties, including Thomas, were described by the Department of Agriculture in a special report (*16*) issued in 1896. One of these was named Peanut because of the more or less cylindrical and peanutlike shape of the single-lobed kernels. So far as is known, with the exception of Thomas, no other of these varieties is now being grown.

The introduction and testing of black walnut varieties received little further attention until early in the present century. It was largely as a result of nut contests begun in 1905 by Morris, and later expanded by the Northern Nut Growers' Association and other organizations and individuals, that this interest became somewhat general. The industry received its next major impetus about 1915 when the prize varieties were first propagated by nurserymen and made available to the public A large number of promising varieties are now on record. Many of these have been propagated to some extent.

Following the lead of Morris in bringing out new varieties, and cooperating closely with him, mainly through the Northern Nut Growers' Association, W. C. Deming, J. Russell Smith, Swarthmore, Pa., the late W. G. Bixby, and the late J. F. Jones conducted many surveys in the East to discover black walnut seedlings suitable for varietal recognition. The Bureau of Plant Industry has participated actively in all of these efforts.

During recent years other black walnut contests have been conducted by the State experiment stations of Michigan, Ohio, and New York, and also by a number of individuals, especially N. F. Drake, Fayetteville, Ark., and H. F. Stoke, Roanoke, Va. In most of the association contests Deming did much of the detail work and participated actively in all judging. In this he was closely followed by Bixby during a period of about 15 years beginning in 1918. Smith took entire charge of advertising the 1926 contest, which was one of the most important ever held by the association. He has been one of the principal judges in several of the contests.

Of the eastern black walnut varieties that have been brought to light in various ways, several are now grown by nurserymen. The best known of these are Creitz from Indiana, Cresco from Iowa, Ohio from Ohio, Rohwer from Iowa, Sifford from Virginia, Stabler from Maryland, Stambaugh from Illinois, Tasterite from New York, Ten Eyck from New Jersey, and Thomas from Pennsylvania. Many other varieties from New York to Arkansas and from Minnesota to Virginia are also being tested, primarily by individuals, although to some extent by public institutions. Many of these merit much greater attention than they are receiving. Unless they are propagated soon, they are likely to be lost.

The Bureau of Plant Industry has made many crosses for the purpose of developing better varieties, but so far all have suffered from adverse circumstances and few nuts have been produced. A small

number of hybrid trees are now growing on the grounds of the United States Horticultural Station at Beltsville, Md. The Minnesota Agricultural Experiment Station is growing many seedlings of certain northern varieties for the purpose of selecting individuals hardy and otherwise of merit in that latitude.

As with the hickories, practically no varieties of black walnut have yet been fully tested in orchard plantings. The shells of all black walnut varieties yet recognized are much too thick to be cracked except by mechanical means, although some shells are less thick than others.

Butternut

What has been said concerning the varietal status of the eastern black walnut is largely applicable to the butternut, *Juglans cinerea* L., although considerably less progress has been made in the development of choice varieties. This species has a rather restricted range within the Eastern States, but it occurs naturally as far west as eastern Nebraska. At present it is nowhere abundant over large areas. As a tree it does not equal the black walnut in size, although in a favorable environment it sometimes reaches 100 feet in height and nearly 4 feet in trunk diameter. The nuts are oblong, cylindrical, sharp-pointed at the apex, bluntly rounded at the base, rough and jagged over the surface, and usually thick-shelled. Nevertheless some varieties have very good shelling quality and the majority have kernels with a rich, agreeable flavor. In cooking and in the manufacture of confections the butternut shares the popular favor of the black walnut.

The first variety of butternut to be named seems to have been Aiken, discovered in 1917 by S. E. Aiken, Grasmere, N. H. It was first propagated in 1918 by J. F. Jones, Lancaster, Pa. Other varieties have since been found mainly as a result of contests held by the Northern Nut Growers' Association, but none have been commercialized.

While most varieties of butternut have thick shells and are difficult to crack, some crack so well with hand-power machines, of which several are on the market, that the kernels are released in unbroken halves.

This species has been greatly neglected by horticulturists. Besides producing nut kernels of excellent quality the species is the hardiest member of the walnut genus, its native range extending well into Canada. It is abundantly worth development wherever it succeeds, especially in the North.

Japanese Walnut

The Japanese walnut, *Juglans sieboldiana* Maxim., was first introduced into this country about 1860. It has since been widely tested in practically all parts of the country without anywhere attaining great importance. The tree has much the size and general form of a large apple tree. Its nuts are of two distinct shapes, and botanists at one time thought there were more than one species. One of these was called *J. cordiformis* Maxim., literally "heart shaped", from the shape of the nuts. However, there is but one species, as the tree characteristics are identical, and seed nuts of either type produce offspring of both fruit types as well as of many intermediate forms.

The nuts of both types are smaller, of smoother surface, and with somewhat thinner shells than eastern black walnuts. In general, both Japanese walnut types are top-shaped and sometimes sharply pointed at the apex. Those once called *Juglans cordiformis* are now known as heartnuts. These are the better of the two and are now receiving the attention of horticulturists. The late J. F. Jones propagated a number of varieties, beginning in 1918 with one that he called Lancaster. Somewhat later he introduced Bates, Faust, and Ritchie. These make quick-growing trees of much ornamental value. The nuts are excellent. Often the flavor is indistinguishable from that of the best butternuts.

The Japanese walnut, the butternut, and the Persian walnut blossom about together and 2 or 3 weeks ahead of the black walnut. Consequently they hybridize freely. The stamens and pistils of individual flowers mature at different times, usually the stamens first, and this, with wind distribution of pollen, tends to promote cross-pollination. By breeding it should be possible soon to develop valuable new forms not grown elsewhere, which would therefore have no competition with others of their own kind either imported or grown in the forests of this country. The hybrids are usually very vigorous and luxuriant in foliage, but fruit setting is sometimes very meager in spite of abundant production of both staminate and pistillate blooms. Size of tree seems to have little relation to the number of nuts produced.

Seedling Japanese walnuts grown in this country often produce nuts greatly resembling butternuts. This occurs with any generation, beginning with direct importations and continuing indefinitely. With imported seed this is undoubtedly due to reversion to a parent type common in the Orient, known as the Manchurian walnut, *Juglans mandshurica* Maxim., which is so much like the American butternut that it is considered to be the same by most travelers from this country. In other cases the resemblance is quite definitely known to be due to hybridization with either butternut or Persian walnut. It is possible that there may be occasional crosses with the eastern black walnut, *J. nigra*, but no case in which this appears probable has come to the attention of the writers.

As a rule the nuts of butternut type borne by possibly hybrid Japanese walnut trees are usually of little value owing to the thickness of the shells and poor quality of the kernels. However, two varieties of apparently hybrid origin with the butternut as a parent are being propagated to some extent. These are Helmick from Iowa and Creitz from Indiana. The former is a discovery of James K. Helmick, Columbus Junction, Iowa, and the latter was brought out by W. A. Creitz, of Cambridge City, Ind., after whom a variety of black walnut was also named.

Persian (English) Walnut

The Persian (English) walnut, *Juglans regia* L., is the best-known and most widely grown nut-bearing species of the North Temperate Zone. The tree is handsome, large, and of great value wherever it succeeds, both on account of the nuts it produces and for its timber. It is native to western and central Asia. Its nuts form an important

article of food and of general commerce. Production is important in California, Oregon, and to some extent in Washington in this country, in many European countries, in China, and to some extent in Chile.

The origin and early history of this walnut is concisely given by Heiges (*16*), who wrote:

> It was known to the Greeks, who introduced it from Persia into Europe at an early day as "Persicon" or "Persian" nut and "Basilicon" or "Royal" nut. Carried from Greece to Rome, it became *Juglans* (name derived from *Jovis* and *glans*, an acorn, literally "Jupiter's Acorn" or "Nut of the Gods"). From Rome it was distributed throughout continental Europe.

It reached England prior to 1562. There seems to be no clear record of the first introduction of this walnut into the United States, but occasional references and other evidence indicate that it came with the earliest settlers. Robbins and Ramaley (*31*) state that "In colonial days, the term English was used to distinguish this walnut from the native American black walnut and because at that time the nuts were imported via England."

At present Persian walnut trees occur quite frequently along the Atlantic seaboard from Long Island Sound west to Rochester, N. Y., and south to Virginia. Old trees, mostly in decrepit condition, are not uncommon. What is perhaps the oldest if not the largest Persian walnut in the United States stands on what is known as the Jacob Bauder farm, 7½ miles northeast of Reading, Pa. This tree was discovered in 1922 by the late J. F. Jones and was determined by him to be 210 years old. It measured 15 feet 1 inch in circumference at 4 feet from the base and had a limb spread of 90 feet. It is supposed to have been planted by the earliest German settlers.

Under the heading "A Giant English Walnut", the American Garden for September 1888 gave an account of a number of Persian walnut trees, one of which was still standing at that time and had been part of a planting by Roger Morris, an English gentleman, who in 1758 built a spacious mansion on his estate on Manhattan Island. The supposition is that the trees may have come from the Prince Nursery, Flushing, N. Y., which was established in 1713, 45 years previous to the Morris planting.

Other definite evidence of early planting is afforded by the so-called James River Hybrid, which was cut down in 1928. It stood on Rowe Farm, opposite Brandon, near the bank of the James River in southeastern Virginia. This was believed to have been a natural hybrid between the Persian and the eastern black walnut. Its apparent age was estimated by Bisset (*9*), who observed it in 1911, to have been from 150 to 200 years. As the year of Bisset's visit was 304 years after the settlement of the first successful English colony in this country at Jamestown in 1607, it would seem probable that the Persian walnut parent was brought from Europe and established there by colonists some time during the first century of English colonization in this country.

According to Lelong (*21*), the Persian walnut is supposed to have been introduced into California by the Franciscan monks in 1769. He reported that the earliest planting outside of the missions was made in San Diego probably in 1843, and that a second such planting was made near Calistoga in 1848.

The first Persian walnut planting in California to lead to commercial development was made by Joseph Sexton, of Santa Barbara, from nuts presumably of Chilean origin, bought by him in San Francisco in 1867 (*36*). Nuts from the Sexton trees were later used for growing seedlings for extensive orchard plantings in southern California. The nuts from these are known on the market as Santa Barbara soft-shells. Hard-shell walnuts were planted in northern California at about the same time as in southern California. It remained, however, for Felix Gillet, a Frenchman, who established the Barren Hill Nurseries at Nevada City, in 1871, to arouse interest in the whole State in grafted walnut trees of soft-shell varieties. He early imported many shipments of scions and nursery trees and was the first to introduce into California practically all of the best French walnut varieties now grown in this country.

Plantings of seedling Persian walnut trees are known to have been established in Oregon during the seventies or early eighties, as occasional seedling trees estimated to be from 50 to 75 years of age are to be found in the Willamette Valley of that State. The first commercial planting in Oregon consisted of seedling trees put out in 1893 by L. T. Davis, of Dundee, Oreg.[2] This orchard was later purchased by Thomas Prince, by whom it was materially expanded and made famous for many years as the Prince Orchard. Grafted trees began to appear in the Pacific Northwest during the late nineties, when A. A. Quarnberg, of Vancouver, Wash., and others first planted trees of French varieties, which they procured from Gillet.

The practice of breeding walnut varieties by selection appears to have been inaugurated by the French. L. D. Batchelor stated in an unpublished report on walnut culture in France that some of the varieties, such as Mayette and Franquette, had been grafted for over 100 years, and that the present commercial walnut industry of France is based upon grafted walnuts.

The planting of the seedling trees by Sexton was followed by marked expansion of seedling orchards in the southern part of California until about 1900, when many individual trees began to be selected and used as new varieties. Since about 1905 practically all plantings have been of named varieties and many seedling orchards have been top-worked.

In the Eastern States for approximately 10 years, beginning about 1915, efforts were made by J. F. Jones, and others to develop Persian walnut varieties that would be hardy in that section of the country. It was assumed that hardiness would be increased by grafting varieties on stocks of the eastern black walnut, *Juglans nigra*. However, practically all of the varieties so developed have since become obsolete, as they proved too subject to injury by winter cold or late spring freezes. Hardiness was apparently not affected appreciably by the use of black walnut stocks.

Persian walnut breeding by cross-pollination is still in the initial stages. Much preliminary work has been done in the way of conducting studies of blossoming habits and of pollen behavior. Varieties of this species are largely dependent upon other varieties or species of

[2] Personal statement made July 21, 1910, in Washington, D. C., by E. R. Lake, former professor of horticulture and forestry, Oregon Agricultural College, Corvallis.

walnut for pollen for the reason that their own pollen is often not available at the time it is needed. This is because the staminate or pollen-producing flowers do not function simultaneously with the pistillate or nut-producing flowers. Usually in such cases the staminate flowers mature and shed their pollen, dry up, and fall to the ground before the pistillate flowers become receptive. Occasionally, however, this order is reversed and the pollen is shed too late to function on earlier maturing stigmas. Young trees seldom produce staminate flowers until several years after the appearance of the first pistillate flowers. Wood (*46*) has found that varieties of this species are entirely fertile to their own pollen when it is available at the right time, and equally fertile to pollen of any other species of *Juglans*.

Persian walnut hybrids, resulting from natural crosses with the Hinds walnut (*Juglans hindsii*) of northern California, occur with great frequency in that State. In the East natural hybridization is not uncommon with the eastern black walnut (*J. nigra*) or with the butternut (*J. cinerea*) and occasionally with the Japanese walnut (*J. sieboldiana*). No hybrid of these types yet found has been of horticultural value, although often the trees are vigorous growers of much beauty and not infrequently of greatly increased hardiness. No doubt some of these hybrids would furnish timber of value; but the cost of developing hybrids, added to that of bringing walnut trees of any form to timber age, is entirely too great to justify consideration of hybrids for this purpose under present economic conditions. The few nuts produced by these hybrids are usually thick-shelled and contain very little kernel.

Breeding the Persian Walnut

The principal weak points in present varieties of Persian walnuts are susceptibility to bacterial blight, lack of hardiness sufficient for conditions in the Eastern and Northern States, lack of uniformity in bearing, and general lack of quality of nuts. Some varieties have considerable astringency in the pellicle of the kernels, owing to the presence of tannic acid.

Practically all varieties are susceptible to walnut blight, a serious bacterial disease affecting both nuts and twigs. This disease is now being controlled by proper spraying, but only at great expense. Lack of hardiness is a definitely limiting factor in the East, although there are occasional trees in many of the Eastern States. Trees that survive longest in this region usually have the protection of buildings, lakes, or other agencies that modify local temperature extremes. The Persian walnut is quickly responsive to warm periods in late winter or early spring and consequently is vulnerable to frost injury. When injured by frost or other mechanical agency the tree recovers slowly. Loss by freezing is a matter of universal concern in commercial walnut districts of Europe, Asia, and the United States.

Variation in annual yield largely results from environmental influences and would be difficult to overcome or reduce through breeding alone. Nevertheless, it is more serious in some varieties than in others, and development of greater fruitfulness should result in appreciable improvement.

Some varieties are more resistant to blight than others, and because of slow response to mild temperatures, some are less subject to injury by cold in winter or spring. Other superior qualities of some varieties include fruitfulness; uniformity in size of yearly crops; shells well-sealed at the ends and so firm that they do not crack while being handled, although they are easily cracked by machine or hand; very little or no astringency in the pellicle; and richness and palatability of kernel. Such varieties, each having certain good qualities, are the material from which the breeder hopes to develop new varieties having combinations of larger numbers of desirable characteristics.

The problems involved in breeding by cross-pollination are not unusually intricate. While it is possible that better varieties or better basic material for use in breeding, particularly in the matter of hardiness, might be obtained from some foreign country, this does not seem probable, as the principal walnut regions of the world have been fairly well searched. It is believed that an abundance of varieties and strains of types desirable for breeding is already within this country. As a rule French varieties are the hardiest among grafted kinds, although a few seedlings in the East, probably of German origin, may be somewhat more hardy. However, eastern-grown Persian walnuts seldom have the high quality and relative freedom from astringency of pellicle characteristic of the western nuts, such as the French and the Santa Barbara soft-shell varieties.

Persian walnut breeding has thus far been confined to selective methods for developing greater hardiness, greater resistance to blight, heavier bearing habits, and nuts of superior quality. Nuts are desired of large but not too large size, of good sealing quality, and with shells thin enough to crack readily without breaking during normal handling. The kernels must be plump, bright, smooth, free from prominent points that break off easily, rich in quality, sweet in flavor, and without tannic bitterness in any part of the pellicle.

The New York (State) Agricultural Experiment Station has made crosses between *Juglans regia* and *J. nigra* in the hope of developing walnuts of the Persian type hardy at that latitude. Similar crosses have been made by the Minnesota Station at University Farm, St. Paul. In both cases the first-generation offspring has shown increased hardiness as well as vigor, but the nuts have been of little value.

In Mexico a certain amount of breeding by selection and of variety testing is being conducted under the direction of G. Gandara, Secretariat of Agriculture, Department of Stations and Experimental Fields, Mexico, D. F.

Breeding by selection to develop superior or even more hardy varieties of Persian walnut appears to have about reached its practical limit, as the principal walnut-growing regions of the world have been more or less thoroughly surveyed and no new varieties of outstanding merit have been found in considerably more than a decade. However, an effort is now being made by P. C. Crath, of Toronto, Canada, with the financial aid of Carl Weschcke, St. Paul, Minn., to procure *Juglans regia* seed from certain known trees in the Carpathian Mountains of Poland, which, it is hoped, will produce seedlings hardy in northern parts of this country and Canada. Distributions of seed nuts from that source have already been made more or less generally

throughout Wisconsin, Minnesota, the Dakotas, and Ontario, Canada. Reports as to the behavior of resulting seedlings are contradictory, but there is a possibility that some of the Crath introductions will prove suitable for limited use in home plantings where other trees of the same species have not been hardy.

Breeding by hybridization in the hope of developing an entirely new form of walnut, which would be distinctly unlike any existing form and therefore would have no direct competition, is now being planned by the Bureau of Plant Industry for the early future. This is to be undertaken by crossing the Persian walnut with the butternut for hardiness and flavor, and probably with the eastern black walnut for a blend of excellent flavors and possible greater timber value. Crosses will be made so as to include the best of the Japanese walnuts, as that group is more hardy than the Persian walnut and will grow farther south than the butternut. Heartnut trees do not attain the great size of the eastern black walnut, and from that standpoint they are more desirable for orchard purposes.

Hybridization of varieties strictly within the species with possible infusion of characters from some other species on the western coast should greatly improve resistance to disease, hardiness, fruitfulness, and the general quality of nut. However, plans for breeding of this sort do not appear to have been announced by any institution or individual. Nevertheless, the possibilities are so great and the field so inviting that it is hardly to be conceived that it will long remain neglected.

In the appendix are listed varieties of black walnut, butternut, Persian walnut, and Japanese walnut, likely to be of value in breeding work, and the names of plant breeders who are actively working with *Juglans*.

ALMOND

THE almond, *Amygdalus communis* L., is a close relative of the peach and therefore a member of the botanical family Rosaceae. It resembles the peach in appearance of tree, foliage, and flower. It is one of the earliest orchard fruits to blossom. In this country the blooming period is from January to March, and on this account it succeeds only in regions where there is minimum danger of killing temperatures during that period. It requires a definite although short period of complete dormancy, without which it tends to become evergreen. For this reason it is unsuccessful in the mild regions of the South.

Two types of almonds are under cultivation, sweet and bitter. To the former belong the familiar almonds of commerce, common in the markets. Of these there are three types, depending upon the thickness of the shells—hard-shell, soft-shell, and paper-shell. The Jordan is a typical hard-shell variety, the Peerless a typical soft-shell, and the Nonpareil a typical paper-shell. Seedlings of both sweet and bitter almond are used as stocks upon which to bud edible varieties.

Like the Persian walnut, the almond is of Old World origin and has been known and prized for food since the earliest times. It is supposed to have originated in the Mediterranean Basin.

It is not improbable that improvement of the almond by crude selection began quite as early as with any orchard fruit. There is evidence that grafting was practiced long before the Christian

Era. The almond is easy to bud, and it is presumable that in very early times good almonds were worked on those less good and thus perpetuated.

Almond varieties have been recognized as such for a century or more in Spain, but varieties there are types rather than clons. Almonds were first introduced into the eastern United States by pioneer horticulturists, but without success. Later they were taken to California, where, during the last half century, their cultivation has become an important orchard industry. Introductions of varieties of European origin into California began before 1853.

Figure 7.—A. T. Hatch (1837–1910), Suisun City, Calif., greatest contributor to the development of almond varieties in this country. During the eighties he originated the so-called "Hatch varieties" IXL, Ne Plus Ultra, and Nonpareil, which have since been the leading sorts grown in California. At that time these became his final favorites out of many of the first selections made by him from seedlings of a bitter almond tree standing near a sweet almond by which it had doubtless been pollinated.

The first varieties introduced into California proved of little permanent value and have since been gradually supplanted by others of California origin. Out of 76 varieties rated by Wood (*45*) as being of commercial importance in California in 1925, 60 were of California origin, 4 of uncertain origin (probably California), and 12 only were from Europe. None of the European varieties was rated as being then in favor with experienced growers or apparently of value for future use. However, the early introductions and their ill-advised planting in various parts of the State threw much light on the possibilities of almond growing in California and on environmental and cultural requirements, and furnished material for developing better varieties.

Almond breeding by selection from seedlings grown on a large scale for the purpose appears to have long preceded similar work with any other nut grown in this country. In 1878 A. T. Hatch (fig. 7), of California, who at one time had almond plantings in 20 counties put out at Suisun City an orchard of over 2,000 seedlings grown from nuts of a supposedly seedling bitter-almond tree which stood near a tree producing sweet almonds from which its flowers were undoubtedly cross-pollinated.[3] The purpose was to use these seedlings as stocks upon which to bud good varieties. Concerning his next move, Hatch wrote:

I found a supposedly seedling almond which had been prolific in its bearing for several years. It was small but soft-shelled, sweet, but hard to hull and therefore

[3] Letter from Mr Hatch in Department file written June 20, 1892; Nut Culture in the United States (*16, p. 80*); and recent statement by Mrs. P. C. Campbell, Vacaville, Calif, a daughter of Mr. Hatch.

expensive to handle, though I thought it was better than one that did not bear good crops, so I budded the seedling trees in place in the orchard with buds from these trees (probably this tree), but not having buds sufficient for all there were, somewhere near 300 remained seedlings. The second year after planting I found upon some of these a few almonds, some of which seemed to be very fine, sweet, soft-shelled almonds, when I concluded to leave them as seedlings until they might bear fruit.

From then on he marked the trunk of each tree in such manner as to indicate the character of the nuts and size of the crop. It was from trees so marked that he made many selections, including two that he later named IXL and La Prima.

Hatch was so pleased with the general character of the nuts from these unbudded trees that he tried to induce those that he had previously budded to push out sprouts from below the buds in order that they too might bear. In this way he was able to add greatly to the total number of promising new sorts. Among those so discovered were two that he later named Ne Plus Ultra and Nonpareil. These two, together with IXL, were his final selections; and under the popular group name of "Hatch varieties" they later took rank among the most important varieties of almond grown in this country. To some extent these have been introduced into foreign countries.

The great majority of varieties now grown in California originated as chance seedlings discovered by careful observers in various parts of the State. A few were introduced from France, mostly by Gillet. Several came from Spain as the result of introductions by David Fairchild and Walter T. Swingle, of the United States Department of Agriculture. However, next to Hatch it is probable that the man who did most toward contributing valuable varieties to California was A. M. Newlands, of Colusa. Newlands planted a sack of almonds in 1883, and 3 years later chose 4 seedlings, to which he gave the names of California White, Commercial, Eureka, and Lassen (*45*). Of these, Eureka is one of the best small varieties in the State.

Breeding by hybridization was begun by M. N. Wood, of the United States Bureau of Plant Industry, in 1923, in cooperation with the University of California. Thousands of crosses have been made and the resulting seedlings brought to fruiting at the State Agricultural Experiment Station at Davis, Calif. A number of promising seedlings are now under observation. Two of these are being tested in many parts of the State. Nuts from one of these and from both parents are shown in figure 8.

Present Work in Almond Breeding

Few of the varieties producing the best nuts are good bearers. Some of the best bearers are unsymmetrical trees, difficult to prune. The nuts of many of those that bear well have hard shells or are of inferior flavor. The shells of some others are of such softness that they crumble badly in ordinary handling. A considerable portion of the kernels of certain varieties are gummy and objectionable. In many cases the foliage is seriously subject to red spider injury. Some varieties are difficult to "knock" from the trees; that is, to jar off when fully mature. In some varieties there are often a great many "sticktights" or nuts from which the husk separates poorly or not at all. A few of the varieties most extensively grown produce nuts too small to bring good

prices. A not uncommon defect is that of forming double kernels, called "philopenas."

If a variety of almond could be found combining all of the good points of present varieties and seedlings, little more could be desired in the way of a first-class almond. Such desirable characteristics as late blooming; full bearing; good qualities for harvesting, hulling, and

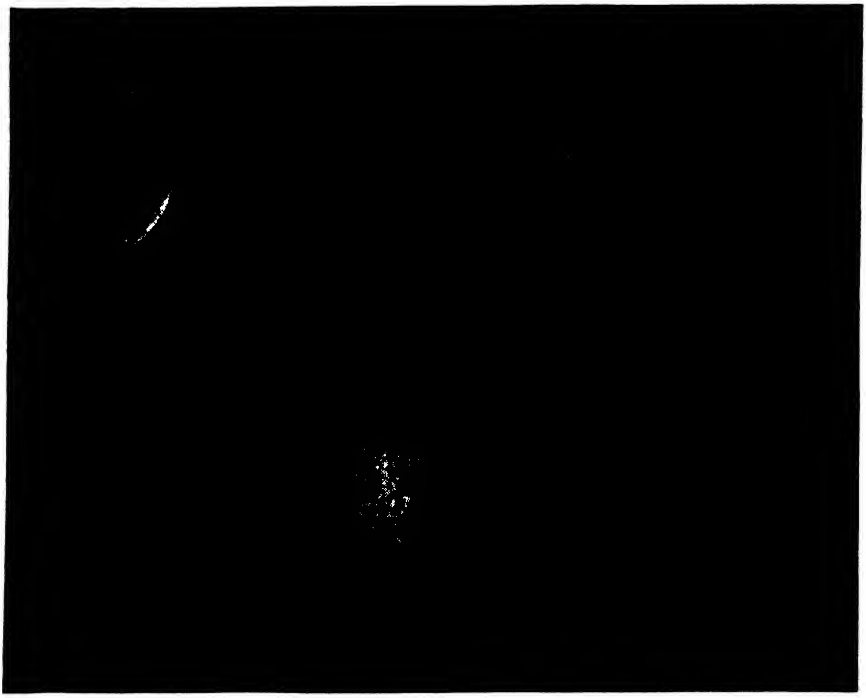


Figure 8.—Two of the almonds used in breeding and their offspring, which is believed to be promising as a new variety: *A*, Pistillate parent; *B*, staminate parent; *C*, the offspring. $\times 2/3$. The nut of the new variety is superior to that of either parent in being larger, brighter in color, and of thinner shell. The kernel is larger, brighter, smoother, and of finer flavor. The tree is more fruitful and so far has been highly resistant to the red spider.

shelling; a high degree of resistance to certain insects, particularly the red spider, and to a number of diseases; and general excellence of kernel, are all to be found distributed among present varieties and seedlings.

The problem of the almond breeder is to combine as many as possible of these good qualities in a few varieties. This should not be difficult, as the technique of almond breeding, like that of other rosaceous fruits such as apple, peach, plum, and others, is not especially difficult to perform. Almond pollen is carried only by insects and not by wind, and pollination is therefore easily controlled. This is quite different from walnuts, hickories, chestnuts, and filberts, the pollen of which is wind-carried, produced in great abundance, and difficult to control.

Present work in almond breeding by the Bureau of Plant Industry is well-organized and, as already noted, is being systematically carried on in cooperation with the University of California. Nuts from crosses made by Bureau workers are planted in nursery rows at University Farm, Davis. When the seedlings are 1 year old, scions from some of the more vigorous growers are top-worked in old trees and quickly brought into bearing. Large numbers are soon eliminated and only the most promising are preserved. In 5 to 10 years after the seed is planted further selections are made, and these are tested in various almond sections of the State by top-working on established trees. The work is making very satisfactory progress, although no varieties are yet ready for general distribution.

With the possible exception of certain of the Jordan types as grown in Spain—long, hard-shelled varieties, very popular with confectioners, chiefly because of the form of the kernel—it is generally conceded that the best almonds on the world's markets now come from California. When the good points of the California varieties are rightly combined there is abundant reason to expect that American almonds will completely dominate the markets of this country.

Breeders now engaged in work with almonds are named in the appendix, which also contains a list of almond varieties considered valuable as breeding material.

PISTACHE

THE pistache, *Pistacia vera* L., is a small-growing, wide-spreading tree up to 30 feet in height, dioecious in habit of flowering, and producing nuts of much value. The nuts are small in size and borne in clusters that often weigh several pounds. Each nut has a thin, reddish, leathery husk. The shell of the nut is very smooth, whitish, and thin, yet of bony hardness. It tends to split open slightly upon maturity, but not to such extent as to release the kernel. The flavor is mild, the texture fine, and the color of the kernel greenish throughout. When finely ground, pistache kernels are used to give color and flavor to confections. The darker they are the better they suit the purpose. The nuts are prepared for market by salting and roasting while still in the shell.

The pistache grows in hot dry regions where it withstands adversity better than either the almond or the Persian walnut. It is native in Syria and nearby regions. It was first introduced into the United States in 1853–54 by the Commissioner of Patents, by whom seeds were widely distributed throughout the Southwest. Little interest was aroused, however, until 1876, when other introductions were made by G. P. Rixford, of San Francisco, Calif., by whom trees were brought into fruit in 1881. Many more recent introductions have been made by the Division of Plant Exploration and Introduction, Bureau of Plant Industry.

There are now numerous small plantings of pistache trees in the interior valleys of central and southern California. For many years the most extensive grower in that State was Claude Tribble, of Elk Grove. He made many experiments in propagation, including the use of different species as stocks upon which to graft the better varieties. In his experience *Pistacia atlantica* Desf. proved more satisfactory than *P. chinensis* Bunge. Others have used *P. terebinthus* L. as a stock with satisfactory results.

Much work is still necessary to determine the most satisfactory pollinizers to use for the cultivated varieties. Practically no work in breeding has yet been reported and so far as known none is planned for the immediate future. However, the superior merit of this species and its ability to grow under conditions to which no other nut of this country is well adapted would seem to justify immediate attention by our breeders.

THE TUNG TREE

The tung tree, *Aleurites fordii* Hemsl., is the hardiest and most valuable member of a group of closely related tropical and subtropical trees producing inedible seeds or nuts from which a valuable drying oil is extracted. This oil has been used in the Orient for many centuries in waterproofing wood, paper, fabrics, and other products. Within the last half century it has come into important use in Europe and the United States in the manufacture of waterproof varnishes, paints, paint dryers, and linoleum. Tung oil is much like linseed oil but dries more rapidly and is more resistant to water. The tree is handsome, having a round top and dense, catalpalike leaves.

The species was introduced into the United States in 1905 by the Division of Plant Exploration and Introduction through the efforts of David Fairchild, then in charge, and United States Consul General L. S. Wilcox, Hankow, China. It has since attracted wide attention among planters in northern Florida, southern Georgia, and Gulf Coast States westward to Texas.

The earliest plantings were entirely of seedlings chosen without regard to hardiness, fruitfulness, or merit of nuts produced. In 1923 studies as to relative merits of strains and seedlings were begun by the Florida Agricultural Experiment Station at Gainesville. Later, similar work was taken up by the State stations of Georgia and Louisiana and by certain individuals, notably the late J. B. Wight, Cairo, Ga. Several selections have been made, and in a few cases these have been placed on a varietal basis by budding and grafting in the nursery. One commercial orchard of grafted trees consisting of about 4 acres has been established at Cairo, Ga.

The Florida station found that seed nuts planted in early winter or midwinter often result in trees ranging from a few inches up to 6 to 8 feet in height by the end of the first season. Such large trees may be budded during the late summer or fall. The buds will remain dormant until the following spring, when the tops should be cut back and the buds made to push out. In this way budded trees suitable for transplanting may be grown in about 24 months from the time the seed is planted.

Active hybridization was begun by the Florida station at Gainesville in 1929. Several selections from the resulting seedlings have since been made, but their value has not yet been fully determined. Selective breeding at the Georgia Coastal Plain Experiment Station, Tifton, Ga., begun in 1933, has resulted in the selection of three promising seedlings, nos. 24, 39, and 49. Breeding through pure-line selection and hybridization was begun at the Louisiana Agricultural Experiment Station, Baton Rouge, in 1935. The objectives at each of the stations are much the same; that is, to produce varieties that are hardy, vigorous, and heavy producers of good nuts rich in oil.

Figure 9.—Nature of growth and blossoming habits of hickories and walnuts as illustrated by the pecan. *A*, Twig showing staminate flowers (*a*) borne axillary on growth of the past season and (*b*) pistillate flowers borne terminally on growth of the current season. *B*, Section of a catkin showing three staminate flowers of the many that form on each catkin. *C*, Enlarged staminate flower containing several anthers (*a*); *b*, sepals. *D*, Single pistillate flower with rough stigma at *a*.

FUNDAMENTALS IN NUT BREEDING[4]

COMPLETE pollen control is vital to efficiency in nut hybridization work. The chief genera grown in this country are walnut, hickory (including the pecan), filbert, pistache, chestnut, almond, and tung. With the

[4] The following pages are intended primarily to give instruction to students and those professionally interested in nut breeding.

exception of almond and pistache, all are monoecious; that is, the pollen and nut-producing flowers form separately in different parts of the same tree, as shown for the pecan in figure 9. The almond bears perfect flowers; that is, stamens and pistils occur in the same flowers, as shown in figure 10. The pistache is dioecious and bears the pistillate and staminate flowers on different trees. In general appearance the tung flowers greatly resemble those of the almond, but they are imperfect, as stamens appear in some flowers and pistils in others. The pollen of almond and tung trees is carried by insects; that of the walnuts, hickories, filberts, pistaches, and chestnuts is carried by wind.

Figure 10.—Essential parts of an almond blossom: *a*, Stigma; *b*, style; *c*, ovary; *d*, anther; *e*, filament.

In most wind-pollinated nut-bearing species, dichogamy exists to a greater or less extent. This development and maturity of the staminate (male) and the pistillate (female) flowers at different times necessitates cross-pollination. The degree of dichogamy varies with the variety, the age and nutrition of the tree, and seasonal conditions. In the case of some varieties of the same or different species, dichogamy is so complete that the trees are unfruitful unless they are pollinated by another variety producing pollen at the time the pistils are receptive. Some varieties are protandrous, that is, mature their pollen in advance of the period of stigma receptivity of the pistillate blossoms; while others are protogynous, that is, the stigmas of the pistillate flowers are receptive before pollen is matured. In other varieties there is a short and inadequate overlapping period of pollen shedding and stigma receptivity. Therefore, the degree of dichogamy in the material worked is of considerable importance in nut-breeding operations and technique. In the case of the protandrous varieties pollen must be so collected and stored that it will retain its viability until it can be used for selfing or for pollinating other varieties with later pistillate blossoms. The protogynous varieties present a different problem in that the development of the staminate flowers must be forced by cutting off catkin-bearing shoots and storing them in water in a warm place, or by obtaining pollen from localities where the varieties blossom earlier in the season.

Procuring pollen is quite easy, since all that is necessary is to collect the mature catkins just prior to the liberation of their pollen and to place them on smooth, hard paper in a warm, dry room, where the locules will soon open and release the pollen.

The stage of maturity of pollen can be determined by the stiffness of the catkins and the color of the anthers. Woodroof and his coworkers (*49*) found that a pecan catkin that will not shed pollen within 48 hours is relatively stiff, while one that will do so in 12 hours is limber. The color of the anthers until within about 48 hours of the time when they will begin shedding pollen is about the same as that of the leaves and bracts. After that the green color is gradually replaced by the orange yellow of the pollen. This description of pecan catkins applies in general to those of other species of *Hicoria* as well as to *Juglans*, *Corylus*, and *Castanea*.

In order to get a controlled cross it is necessary to use unmixed pollen. This is probably best procured by collecting mature catkins shortly before any pollen has been shed, washing them repeatedly with running water, removing the excess water with a sterile towel, and then drying the catkins slowly in a desiccator or other similar container. The catkins should not be too green, as they will be likely to wilt without shedding, or the viability of the pollen may become impaired.

With some species pollen loses its vitality quickly. In making crosses it is not infrequently necessary to preserve pollen for some time while waiting for the pistillate flowers of desired varieties to mature. To do this successfully, pollen that is thoroughly dry, yet fresh, must be placed in vials or tubes plugged with cotton and held at a low but not freezing temperature.

Figure 11.—Instrument consisting of a hypodermic needle attached to a rubber bulb by means of a curved glass tube, used by pecan breeders in applying pollen to the stigmas of pistillate flowers enclosed within cellophane covers.

Numerous methods have been used for controlling pollination in the wind-pollinated nut plants. Absolute control in such cases is quite difficult and requires a special technique not needed with insect-pollinated plants. It is essential that the pistillate blossoms be covered well in advance of their receptivity with a material that will preclude pollination. These covers must not be removed, even momentarily, while there is pollen in the air. In the pecan it has been shown that pollen is not shed when the relative humidity is about 85 percent; however, that does not insure that the air is free of pollen, for the reason that it may not have had time to settle out. Woodroof (*47*) found that the usual methods of covering the pistillate flowers with cloth bags or paper sacks do not eliminate all possibility of the entrance of pollen. Their findings were later supported by investigations of Traub and Romberg (*40*). These latter workers devised a method of using closely woven cloth bags impregnated with paraffin to cover the pistillate blossoms. A hypodermic needle

attached to a rubber bulb (fig. 11) was used to introduce the desired pollen by simply pushing the needle through the cloth bag and lightly squeezing the bulb to force out the pollen. They also found that if the covers were removed and the blossoms pollinated between 5 and 7 a. m., when the relative humidity was about 85 percent, there was little danger of contamination. Later Smith and Romberg (*34*) improved the method by using transparent cellophane bags made from sausage casings. Since this method of pollination control is readily adaptable to all walnut and hickory species, it will be described in some detail. Cellophane sausage casings are made in many different sizes; usually a casing 1⅛ inches in diameter is satisfactory. These casings are seamless tubes, usually sold in lengths of approximately 32 feet. They are cut to the length desired, and one end is closed by tying, folding over, and tying again. The finished case or tube should be 4 to 5 inches long. The tubes are placed over the clusters of pistillate flowers well before the stigmas become receptive. A plug of cotton batting is wrapped around the blossoming shoot so that the lower end of the tube can be tied over it (fig. 12). The cotton plug provides ventilation for the pistillate flowers. When the stigmas become receptive they are pollinated with the desired pollen by pushing the hypodermic needle through the plugs and blowing pollen over the stigmas by pressure on the rubber bulb in which the pollen has been placed. Separate needles and bulbs must be used for each variety of pollen, or if the same outfit is used it must be sterilized with 95-percent ethyl alcohol and carefully dried when changing from one variety of pollen to another.

Figure 12.—Cellophane cover cut from a sausage casing, used in preventing unwanted pollen from reaching the stigmas of pistillate pecan flowers to be used in breeding. This is plugged with cotton at the lower end and tied tightly at the upper end. The pollen is applied by means of a hypodermic needle (fig. 11) driven through the cotton.

Pollination control in the almond is quite simple. The flowers are emasculated by the removal of the stamens and petals before any

pollen is shed. In practice the emasculated flowers are usually covered with manila bags, or the trees are enclosed in tents or cages made of muslin or wire screen of fine mesh, to prevent the introduction of foreign pollen by insects. However, these safeguards are probably unnecessary, since in rosaceous fruits, including the almond, there is practically no wind pollination and insects do not visit emasculated flowers. When the stigmas of the almond are receptive they are pollinated by being dusted with the desired pollen applied with a camel's-hair brush.

Stigma Receptivity, Pollen Shedding, and Pollen Viability

There are no available data for some of the species of nut-producing plants on the period of stigma receptivity, the time of pollen shedding and pollen viability, and the factors affecting them. In some cases investigations on these points are under way but incomplete.

The almond has a relatively long blossoming period, especially if the time is counted from the opening of the first blossoms of the earliest varieties to the last shedding of pollen by the latest varieties. Tufts and Philp (*41*) report that in practically all instances the first pollen produced was found inferior in quantity and in viability to that produced later by blossoms on the same trees. The abundance and viability of pollen was found to vary with the variety and from season to season, but generally pollen was abundant and viable. The viability of pollen was found to be greatly affected by wind, cold, and rain.

The filbert normally has a long blossoming period, often extending, within the same variety, for more than a month, although when temperatures are unseasonally high it may be short. According to Schuster (*32*), either the filbert stigmas are receptive long before they attain full size or pollen that lodges on their surfaces remains there in viable condition until the stigmas become receptive. The quantity of filbert pollen produced varies greatly according to variety, temperature, and vigor and general condition of tree, and no doubt it is influenced by other factors. The catkins begin to form in summer, and there is great danger of their being injured or killed during the following winter. For these reasons filbert pollen often shows great differences in viability. Schuster found that pollen stored in an open vessel lost less than 25 percent in viability in 2 weeks.

Normally the pecan, as well as other species of *Hicoria*, produces enormous quantities of pollen. Young trees generally produce catkins for one or more years before any pistillate blossoms are formed. Woodroof (*49*) reports that a single pecan catkin will normally shed pollen for 2 days, a single tree for 5 to 6 days, and a single variety for 10 or 12 days. Conditions that are optimum for pollen shedding tend to be destructive to its viability.

In order to gain some idea of the quantity of pollen produced by a single pecan tree, Woodroof (*48*) made detailed observations and counts on a 13-year old Mantura tree that had a total of 941 shoots on which there were 44,885 catkins. These catkins had

approximately 14,241,334 anthers that contained an average of 2,064 pollen grains each. The estimated number of pollen grains produced by the tree, therefore, was 29,394,113,376. He points out that had it been possible for each pollen grain to produce a nut, this tree would have supplied sufficient pollen for slightly more than 229,000 tons of nuts.

The viability of pecan pollen varies greatly with varieties, seasonal conditions, and other factors. Some years a high percentage of the pollen is defective, while in others it is mostly viable. Woodroof (*49*) stored pollen of 20 varieties under 10 different conditions of temperature and humidity and reported that "no temperature and humidity condition was found under which pollen could be stored for longer than 96 hours with certainty of germination." Smith and Romberg (*34*) report that Success pollen from a healthy, vigorous tree, stored at laboratory temperatures for 12 days, still gave a set of nuts, but that under similar conditions Schley pollen remained viable for only 8 days.

Under the humid conditions of Georgia the normal period of stigma receptivity of pecans was shown by Woodroof (*49*) to be about 5 days, but he pointed out that in rainy or cloudy weather the stigmas might remain receptive for 10 to 15 days. Smith and Romberg (*34, 35*) found that under the relatively dry conditions of Texas this period ranged from 12 to 28 days. All unpollinized nuts were found to drop in 5½ to 6½ weeks after the last receptive date.

Walnuts also produce enormous quantities of pollen. Wood (*46*) working with the Persian walnut found that in dry California a single catkin produced from 1 to 4 million pollen grains, and that a single tree would produce from 1½ to 40 billion pollen grains in a single season. A single stigma has a surface area of 10 to 50 square millimeters, yet he found the average number of pollen grains distributed per square millimeter per 24 hours, when pollen shedding was at its height, to be as follows:

	Number
Directly under the trees	8.0
60 feet from nearest tree	4.0
150 feet from nearest tree	2.9
500 feet from nearest tree	1.0
1,000 feet from nearest tree	.3
½ mile from nearest tree	None

Woodroof (*49*) on the other hand, found that in humid Georgia, pecan pollen was carried in appreciable quantities for a distance of 3,000 feet, which would indicate that pecan pollen is lighter than walnut pollen and may be carried considerably farther.

Individual walnut catkins were found by Wood to shed pollen during 4 to 6 days, but under conditions of hot, sunny weather, such as normally prevails in the interior valleys of California at the time walnuts are in bloom, shedding is often limited to 1 day. There is a rather wide range in the development of the different catkins on the same tree, and therefore the pollen-shedding period is much longer than the time indicated for a single catkin. Wood (*46*) found great variation in the viability of walnut pollen. Some pollen grains were devoid of protoplasmic content, and others that appeared normal failed

to germinate. The percentages of germinating pollen grains for different varieties varied from 0 to 80 percent, the average being 23 percent. Under field conditions the Persian walnut pollen loses its viability within a few days after being shed from the anther. Artificially it may be preserved best when kept in glass vials stoppered with cotton and containing a small piece of the catkin to supply moisture to the air in the vial. When kept in this manner and stored in a cool, dry place, in many instances it remained fit for artificial pollination for 3 or 4 weeks. In other cases viability was completely lost within 2 weeks.

Walnut stigmas usually remain receptive for several days, depending largely upon weather conditions. Wood (*46*) obtained the best results from the application of pollen when fluid was being secreted by the glandular portions of the stigmatic surface

Fertilization of Ovule and Development of Embryo

Among nut-producing plants, with the exception of the filbert, pecan, pignut, and Persian and Manchurian walnuts, very little is known regarding pollen-tube growth, ovule fertilization, or embryo development. Even in the case of the species studied there is not complete accord in the conclusions reached by different workers, and such information as is available is far from complete.

According to Benson (*7*), the filbert pollen grain germinates by developing a short tube, which enters the basal region of the stigma. Here the sperm nuclei enter a resting stage, remaining in this condition for 4 to 5 months. During this time the megaspore completes its development, after which the pollen tube resumes its growth and the fertilization of the egg occurs.

According to both Billings (*8*) and N. C. Woodroof (*50*), numerous pecan pollen grains germinate on the surface and send tubes into the stigmatic tissue. The tubes do not enter the stylar canal but grow downward in the tissue on each side of the micropyle and enter the ovary cavity at a point nearly opposite the chalaza. The pollen tubes enter the cavity from 6 to 12 hours after pollination, but they do not enter the embryo sac until about 2 weeks later. The actual fusion of the egg and male nuclei probably occurs about 2 to 3 weeks later, or from 8 to 9 weeks (*2, 50*) after pollination. The first division of the fertilized egg occurs about 2 or 3 weeks later, or about 2 months after pollination.

Shuhart (*33*) reported that pecan pollination generally takes place at the time of the differentiation of the eight nuclei of the embryo sac, and that fertilization takes place about 2 weeks later. However, the stage of embryo-sac development at the time of pollination varies greatly with seasonal conditions and to some extent with the variety.

Langdon (*20*) reports that in the pignut, *Hicoria glabra* (Mill.) Britton, the megasporocyte has reached the megaspore stage or one of the early stages in gametophyte development at the time of pollination. The interval between pollination and fertilization is from 16 to 18 days, while the first division of the fertilized egg occurs about 3 weeks after fertilization or 5 weeks after pollination. In the pecan N. C. Woodroof (*50*) reports the first division of the egg at 8 to 9 weeks after pollination, and Shuhart (*33*) 3 to 4 weeks.

Nast (*22*) found that the complete development from the megaspore mother cell to the one-celled embryo in the Persian walnut, *Juglans regia*, occurs within 7 to 12 days, depending on the season and climatic conditions. Fertilization of the ovule was found to take place 2 to 5 days after pollination.

In the Manchurian walnut *Juglans mandshurica*, it is reported by Langdon (*20*) that the megasporocytes pass through the different phases of meiosis within 3 to 4 days and the embryo sacs are in one of the earlier stages of nuclear division at the time of pollination. After pollination from 4 to 5 days are required for the pollen tubes to reach the embryo sacs, and fertilization of the eggs occurs 1 day later. She found that the fertilized eggs had not divided 12 days after pollination but in material collected 5 days later or 17 days after pollination four 8-celled embryos were present.

Chromosome counts have been made for a number of the nut-producing species, and these are given in table 1, in the appendix.

Incompatibility

Except in the almond and the filbert, incompatibility, or inability of male and female cells to unite and form a fertilized egg that can grow to maturity, has not been definitely shown to exist between individuals within a variety, or between different varieties, or between species of the same genus of the nut-producing plants of the United States.

Tufts and Philp (*41*) found that at least in certain years all almond varieties studied were self-sterile. Of many thousand reciprocal crosses made by them, only the IXL × Nonpareil and Languedoc × Texas seemed to show distinct evidence of incompatibility or intersterility. The parentage of almond varieties now grown in the United States is unknown, and it is therefore not possible to determine whether relationship is a factor in this incompatibility between varieties. Since these few cases of intersterility have been definitely established, it is reasonable to assume that future investigations will disclose further instances of this kind.

In some cases chestnut trees, particularly of the American sweet species, *Castanea dentata*, that grow at a distance from others have been observed to yield unsatisfactory crops or are unfruitful, although producing staminate and pistillate flowers. Such trees apparently require cross-pollination to insure fruitfulness. This is especially true on the Pacific slope, where isolated trees that are fruitful are said to be rare. Stout (*37*) reports observations made on two chestnut trees growing apart from each other at Claremont, Calif., in which the trees were heavily loaded with burs, but those of one tree contained only shriveled nuts without kernels or embryos, and in the several bushels of burs from the other tree there were only about 30 nuts that contained kernels.

Self-unfruitfulness in the chestnut, especially the American species, may be due to either self-incompatibility or to dichogamy. The former condition is indicated by the report of Powell (*26*) in which he suggests that the pistillate flowers are probably pollinated by the staminate blossoms produced on long, slender axillary catkins, which blossom first, and also by those that are produced at the distal end of the pistil-

late catkin and blossom later. He also reports having noticed that most of the stigmas of both European and Japanese varieties are receptive while the early staminate flowers are in bloom.

Schuster (*32*) found that all varieties of filbert investigated by him are practically self-incompatible. While a planting of a single variety will generally produce a few nuts, the quantity attaining maturity is negligible in proportion to the number of pistillate blossoms. Cross-incompatibility was found to exist between a number of varieties. As with the almond, the parentage of the varieties of filbert now grown is uncertain, and therefore no correlation between relationship and cross-incompatibility can be made. Schuster found Du Chilly, which is of the species *Corylus avellana*, to be cross-incompatible with *C. colurna*. He also found *C. colurna* to be nonreceptive to pollen of either Barcelona or Nottingham, both of which are of the same species as Du Chilly. Du Chilly and Barcelona were unfruitful when pollinated with *C. californica*. Reed (*1*) reported that the filbert breeding work of the late J. F. Jones showed that a large number of varieties of the European filbert, *C. avellana*, were definitely unfruitful and none were found to be fruitful when pollinated with pollen of Rush, *C. americana*, but the reciprocals of these crosses were highly fruitful. Reed (*27*) has reported successful pollination of Rush and Littlepage varieties of the American hazel with pollen of *C. colurna*, *C. maxima*, and *C. heterophylla*.

Inheritance of Characters

Most if not all varieties of the nut-producing species as they are grown in the United States are genetically in a complex heterozygous condition. This is due to the fact that all varieties of certain species are self-incompatible, requiring cross-pollination in order to set fruits; or they are dichogamous to a greater or less degree. Thus the nut-producing species do not lend themselves to a study of the inheritance of characters. In most cases several years' time must elapse from the planting of the seed until the resulting seedling produces fruit, and each plant at the time of fruiting requires a considerable area of land, which greatly limits the number of individuals that can be grown under uniform conditions. Nevertheless nut improvement through breeding by hybridization and selection has tremendous possibilities for those who have the inclination, the time, and the facilities to carry on the work.

Very little is known regarding the inheritance of characters in any of the nut-producing species. Some study of hybrids between varieties has been made in the case of the almond, and of hybrids between species in the case of the chestnut. Since 1923 the Bureau of Plant Industry and the California Agricultural Experiment Station have been cooperating in an extensive almond-breeding project. Although the total number of almond trees grown in this project has been large, the number of individuals from any one cross is too small to establish definite genetic ratios with accuracy. However, many interesting facts have been recorded. The factor for bitterness in the nut appears to be present as a recessive in all varieties of sweet almond. In most instances when two sweet varieties are crossed, about three-fourths of the progeny will produce sweet nuts and the rest bitter nuts, giving

a genetic ratio of 3:1. In some crosses, however, the ratio is apparently 1.5:1 or 1:1. Other ratios may be found as the breeding work progresses. The factor for "red spider resistance" seems to be present in some varieties and not in others. To date, red spider-resistant progenies have resulted only from crosses involving Harriott, Eureka, Golden, Nugget, Nonpareil, and Reams. In Jordan the factor for hard shell seems to be dominant. The desirable factor of heavy bearing and the undesirable one of double kernels come out strikingly in Lewelling. From a practical standpoint the results to date show that a prime prerequisite for successful improvement in the almond by hybridization includes the discriminating selection of parents that possess outstanding characters of merit.

Beginning in 1894 and continuing for many years, Van Fleet (*42*) grew many chestnut seedlings from seeds produced by hybridizing *Castanea dentata*, *C. pumila*, *C. sativa*, *C. crenata*, and varieties of these species. Detailed records were not kept, but his work showed certain things of great importance to the chestnut breeder. Hybrids between the chinquapin, *C. pumila*, and the Asiatic chestnut, *C. crenata*, often produced nuts the second year after planting the seed. Apparently the habit of *C. dentata* of coming into bearing much later appeared in hybrids between this species and *C. crenata* or *C. sativa*, since they rarely set burs until they were 5 to 12 years old. Resistance to chestnut blight, *Endothia parasitica* (Murr.) P. J. and H. W. Anderson, was found only when the Asiatic chestnut was used as a parent, and even then when either *C. dentata* or *C. sativa* was a parent the progeny was susceptible. The chinquapin is measurably resistant to blight, but when it was crossed with *C. sativa* or *C. dentata* the progeny was readily susceptible. Detlefsen and Ruth (*12*) made studies of various taxonomic characters in three generations of chestnut trees resulting from *C. dentata* × *C. crenata* crosses made and grown by George W. Endicott, of Villa Ridge, Ill. The striking variations shown by the progeny indicate that many factors are concerned in the inheritance of the characters observed.

So far as is known, the only comprehensive attempt made to improve the European filbert, *Corylus avellana*, by hybridization was by C. T. Brixey, of Gervais, Oreg., who grew about 5,000 seedling trees, mostly from seeds produced by controlled cross-pollination. Out of these, only one seemed worthy of propagation. He named this Brixnut. Only first-generation seedlings were grown, and no effort was made to determine the dominance or recessiveness of the parental characters. Of approximately 2,500 controlled crosses made in the East by Reed (*27*) in 1927 between varieties of this species, because of cold injury only about 50 seedlings have survived. No study of inheritance has been possible.

Reed (*27*) reports that hybrids between *Corylus americana* and *C. avellana* seem to be much more hardy than the pollen parents and are less inclined to sucker, more erect in habit of growth, more vigorous, and more easily trained to tree form than are the pistillate parents. The foliage of the trees is usually like that of the pollen parents, as the leaves are thicker, darker, and stiffer than those of the pistillate parents. The size, form, color, thickness of shell, and plumpness and

appearance of kernel are much like those of the pollen parent. The Rush variety, which was principally used as the pistillate parent, has the highly undesirable character of not permitting training to a single stem. The great majority of the hybrids yield satisfactorily to the single-stem method of training.

Although hybridization of pecan varieties has been carried on for several years by the Bureau of Plant Industry and by pecan growers, very little is known about the inheritance of characters. In most cases only first-generation hybrids have been grown; however, it seems that in cases where one of the parents is susceptible to pecan scab the progeny are likewise susceptible with few if any exceptions. Furthermore, the character of a speckled seed coat, which is characteristic of the variety Brooks, appears in most of the progeny in which Brooks is one of the parents.

The only study known to the writers of inheritance of characters in the genus *Juglans* is that of Babcock (*4*), who studied the inheritance of the peculiar oaklike character of *J. californica* var. *quercina* Babcock in progenies from controlled crosses. The first-hybrid generation seedlings were all typical *J. californica* trees, and of 18 second hybrid generation seedlings grown, 12 were *J. californica* and 6 were *J. californica* var. *quercina*, or a ratio of 2:1. Later backcrosses of the first generation on *quercina* gave approximately 1:1 segregation (unpublished). Because of a widespread belief that the *quercina* type was the result of natural crosses between *J. californica* and *Quercus agrifolia* Nee., many controlled crosses were attempted between these species without any fruit being produced. Thus Babcock concludes that the variety *quercina* probably originated as a mutation.

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APPENDIX

Table 1.—*Number of somatic chromosomes in certain nut-producing plants*

Common name	Scientific name	Somatic chromosome number (2n)	Authority[1]
Almond	*Amygdalus communis*	16	(*10, 11, 19, 24, 25*)
Chestnut:			
American	*Castanea dentata*	24	(*18*)
Spanish	*Castanea sativa*	24	(*18*)
Filbert	*Corylus avellana*	[2] 28	(*51*)
	Corylus avellana var. *pontica*	28	(*51*)
Giant	*Corylus maxima*	[2] 28	(*51*)
Hazelnut:			
American	*Corylus americana*	[2] 28	(*51*)
Tree	*Corylus colurna*	28	(*51*)
	Corylus heterophylla	28	(*51*)
Beaked	*Corylus rostrata*	[2] 28	(*51*)
Japanese	*Corylus sieboldiana*	28	(*51*)
Tibetian	*Corylus tibetica*	28	(*51*)
Hickory:			
Bitternut	*Hicoria cordiformis*	32	(*52*)
Mockernut	*Hicoria alba*	64	(*52*)
Pecan	*Hicoria pecan*	[3] 20–24	(*50*)
Pignut	*Hicoria glabra*	64	(*52*)
Shagbark	*Hicoria ovata*	32	(*52*)
Shellbark	*Hicoria laciniosa*	32	(*52*)
Sweet pignut	*Hicoria ovalis*	64	(*52*)
Walnut:			
Black	*Juglans nigra*	[4] 32	(*51*)
Butternut	*Juglans cinerea*	32	(*51*)
California black	*Juglans californica*	34	(*3*)
Do	*Juglans californica* var. *quercina*	34	(*3*)
Japanese	*Juglans sieboldiana*	32	(*52*)
Manchurian	*Juglans mandshurica*	32	(*52*)
Persian	*Juglans regia*	[4] 32	(*52*)
Texas	*Juglans rupestris*	32	(*52*)
Heartnut	*Juglans sieboldiana* var. *cordiformis*	32	(*52*)
Tung	*Aleurites cordata*	22	(*6*)
	Aleurites fordii	22	(*6, 15*)

[1] Reference is made by number to Literature Cited, p. 957.
[2] Woodworth (*51*) reports: "Three pairs of the gemini commonly fuse completely, so that the metaphase plate appears to have eight small chromosomes and three large ones." In view of this fact Wetzel (*44*) and Jaretzky (*18*) reported only 11 chromosomes as the haploid number.
[3] Because of the small size of the chromosomes the number has not been definitely determined; most probably the base number is the same as for the family.
[4] Nebel (*23*) reports that the somatic chromosome number in *J. regia*, *J. nigra*, and one *J. nigra* × *regia* F_1 hybrid is 34.

Table 2.—*Nut species now being bred, locations, institutions, workers, and methods*

Species	Location	Institution	Workers	Method[1]
Almond	Sacramento and Davis, Calif.	U. S. Department of Agriculture and State Agricultural Experiment Station.	Milo N. Wood	S, H
	Newberg, Oreg.	Private	A. B. Scherf	S
	Sydney, Australia	Department of Agriculture, New South Wales.	H. Wenholz	S
Butternut	Beltsville, Md	U. S. Department of Agriculture.	H. L. Crane, J. W. McKay, C. A. Reed.	S, H
	Geneva, N. Y.	State Agricultural Experiment Station.	George L. Slate	S
	Litchfield, Conn	Private	W. C. Deming	S
	Ithaca, N. Y.	do	S. H. Graham	S
	Cleveland, Ohio	do	C. F. Walker	S
	St. Paul, Minn	do	Carl F. Weschcke	S
	Harrisburg, Pa	do	G. A. Zimmerman	S

[1] S=selection, H=hybridization.

Table 2.—*Nut species now being bred, locations, institutions, workers, and methods*—Continued

Species	Location	Institution	Workers	Method
Chestnut	Glenn Dale, Md	U S Department of Agriculture	R B Clapper, G F Gravatt	H
	Beltsville Md	do	H L Crane J W McKay C A Reed	S, H
	Urbana Ill	State Agricultural Experiment Station	A S Colby	H
	Ettersburg Calif	Private	Albert Etter	S
	Godfrey, Ill	do	Amelia Riehl	S
	Roanoke, Va	do	H F Stoke	S H
	Harrisburg, Pa	do	G A Zimmerman	S
Filbert	Beltsville, Md	U S Department of Agriculture	H L Crane J W McKay C A Reed	S H
	Corvallis Oreg	do	C E Schuster	S H
	St Paul, Minn	State Agricultural Experiment Station	W H Alderman Ernest Angelo, W G Brierly F E Harolson	S
	Geneva N Y	do	George I Slate	S H
	Gervais, Oreg	Private	C T Brixey	S H
	Washougal, Wash	do	D Fitzgerald	S
	Salem, Oreg	do	Pearcy Bros	S H
	Newberg Oreg	do	A B Scherf	S
	College Park Md	do	C P Close	S
	Glenn Dale Md	do	J J T Graham	S
Hickory	Beltsville Md	U S Department of Agriculture	H L Crane J W McKay C A Reed	S
	Urbana, Ill	State Agricultural Experiment Station	A S Colby	S
	Geneva, N Y	do	Geo L Slate	S
	Wooster, Ohio	do	J H Gourley	S
	Litchfield Conn	Private	W C Deming	S
	Ithaca, N Y	do	S H Graham	S
	Downingtown, Pa	do	J W Hershey	S
	Kent, Ohio	do	Homer L Jacobs	S
	Lancaster, Pa	do	Mildred M Jones	S
	Swarthmore, Pa	do	J Russell Smith	S
	Center Point, Iowa	do	Snyder Bros, Inc	S
	Cleveland, Ohio	do	C F Walker	S
	Harrisburg, Pa	do	G A Zimmerman	S
Pecan	Beltsville Md	U S Department of Agriculture	H L Crane J W McKay C A Reed	S, H
	Robson, La	do	F N Dodge	H
	Albany, Ga	do	Max B Hardy, Harry Lutz	H
	Austin Tex	do	C L Smith	S
	Urbana, Ill	State Agricultural Experiment Station	A S Colby	S
	Shattuc Ill	Private	J G Duis	S
	O Fallon Ill	do	Joseph Gerardi	S
	Harrisburg Ill	do	H C Neville	S
	Chetopa Kans	do	Charles Stephens	S
	Rockville, Mo	do	J Tiedke	S
	Rockport Ind	do	J I Wilkinson	S
	Sydney Australia	Department of Agriculture, New South Wales	H Wenholz	S
	Mexico D F	Secretariat of Agriculture Department of Stations and Experimental Fields	G Gandara	S
Tung	Gainesville Fla	State Agricultural Experiment Station	Harold Mowry	S
	Tifton Ga	Georgia Coastal Plain Experiment Station	Otis Woodward	S
	Baton Rouge La	State Agricultural Experiment Station	W D Kimbrough	S
Walnut, Eastern Black	Beltsville Md	U S Department of Agriculture	H L Crane J W McKay C A Reed	S, H
	Urbana Ill	State Agricultural Experiment Station	A S Colby	S
	St Paul, Minn	do	W H Alderman Ernest Angelo W G Brierly F E Harolson	S
	Geneva, N Y	do	George I Slate	S
	Wooster, Ohio	do	J H Gourley	S
	Climax, Mich	Private	Gilbert Becker	S
	Fayetteville, Ark	do	N F Drake	S
	Shattuc, Ill	do	J G Duis	S
	O Fallon, Ill	do	Jos Gerardi	S
	Ithaca, N Y	do	S H Graham	S
	Eldora, Iowa	do	E F Huen	S
	Godfrey, Ill	do	Amelia Riehl	S
	Swarthmore, Pa	do	J Russell Smith	S

Table 2.—*Nut species now being bred, locations, institutions, workers, and methods*—Continued

Species	Location	Institution	Workers	Method
Walnut, Eastern Black—Continued.	Roanoke, Va.	Private	H. F. Stoke	S
	Cleveland, Ohio	do	C. F. Walker	S
	Cincinnati, Ohio	do	Harry R. Weber	S
	St. Paul, Minn.	do	Carl F. Weschcke	S
	Harrisburg, Pa.	do	G. A. Zimmerman	S
Japanese	Beltsville, Md.	U. S. Department of Agriculture.	H. L. Crane, J. W. McKay, C. A. Reed.	S, H
	Litchfield, Conn.	Private	W. C. Deming	S
	Westbank, B. C.	do	J. U. Gellatly	S, H
	Downingtown, Pa.	do	J. W. Hershey	S
	Lancaster, Pa.	do	Mildred M. Jones	S
	Wassaic, N. Y.	do	Gilbert L. Smith	S
	Westfield, N. Y.	do	Ross Pier Wright	S
Persian	Corvallis, Oreg.	U. S. Department of Agriculture.	C. E. Schuster	S, H
	St. Paul, Minn.	State Agricultural Experiment Station.	W. H. Alderman, Ernest Angelo, W. G. Brierly, F. E. Harolson.	H
	Geneva, N. Y.	State Agricultural Experiment Station.	George L. Slate	H
	Roseburg, Oreg.	Private	C. E. Moyer	S, H
	Mexico, D. F.	Secretariat of Agriculture, Department of Stations and Experimental Fields.	G. Gandara	S

Table 3.—*Varieties of nuts of probable value for breeding*

Genus, species, variety, and region	Origin or introducer	Comments
Amygdalus communis:		
Drake	California	Of chief value because of prolificacy and usefulness as a pollinizer.
Eureka	do	Highly prolific, with small but very sweet nuts.
IXL	do	Long one of California's most valuable varieties.
Ne Plus Ultra	do	Do.
Nonpareil	do	Do.
Texas	do	A heavy bearer, considerably like Drake.
Corylus:		
White Aveline	Long a standard; from Europe	Shell very thin; kernel of finest quality and flavor.
Barcelona	do	Leading variety of Pacific Northwest.
Brixnut	C. T. Brixey, Gervais, Oreg.	Large nut; very prolific.
Du Chilly	Long a standard; from Europe	Long a chief variety in Pacific Northwest.
Italian Red	Long well known; from Europe	Has given good results in eastern breeding.
Littlepage	Thomas P. Littlepage, Bowie, Md.	A highly prolific native from southern Indiana.
Rush	J. G. Rush,[1] Pennsylvania	A native found highly useful in breeding.
Winkler	Snyder Bros., Inc., Center Point, Iowa	Best native variety yet found in State.
Hicoria (exclusive of pecan):		
Anthony (probably *H. ovata*).	A. B. Anthony, Sterling, Ill.	An excellent nut.
Berger (probably *H. laciniosa* × *alba*).	Russell Berger, Cove Gap, Pa.	First prize miscellaneous hickories, 1934 contest, Northern Nut Growers' Association.
Chase (probably *H. ovata*).	W. R. Chase, Hartford, Conn.	An excellent nut.
Coleman (probably *H. ovata*).	Mrs. Thomas Coleman, Saltsburg, Pa.	Third prize, 1934 contest, Northern Nut Growers' Association.
Davis (probably *H. ovata*).	Dwight Davis, Dover Plains, N. Y.	First prize, 1934 contest, New York State.
Emerick (probably *H. ovata*).	Etta Emerick, West Camp, N. Y.	Superior cracking quality.
Fox (probably *H. ovata*).	Roland D. Fox, Fonda, N. Y.	First prize, 1934 contest, Northern Nut Growers' Association.
Goheen (probably *H. ovata*).	Mrs. Martha Goheen, Pennsylvania Furnace, Pa.	Second prize, 1934 contest, Northern Nut Growers' Association.
Hagen (probably *H. ovata*).	Mrs. C. E. Hagen, Guttenberg, Iowa	One of the best known in the State.

[1] Deceased.

TABLE 3.—*Varieties of nuts of probable value for breeding*—Continued

Genus, species, variety, and region	Origin or introducer	Comments
Hicoria (exclusive of pecan)—Continued.		
Heibner (probably *H. ovata*).	Harvey A. Heibner, Danville, Iowa	Very superior nut.
Jolliffe (probably *H. ovata*).	George C. Jolliffe, Uffington, W. Va	Very high percentage of kernel.
Lawson (probably *H. ovata*).	Donald Lawson, Dorloo, N. Y	Second prize, 1934 contest, New York.
Mann (probably *H. ovata*).	Mrs. Rae D. Mann, Davison, Mich	First prize, 1932 contest, Michigan.
Miller (probably *H. ovata*).	D. P. Miller, North Branch, Mich	Second prize, 1932 contest, Michigan.
Redcay (probably *H. laciniosa*).	Adam Redcay, Lititz, Pa	Second prize, miscellaneous hickories, 1934 contest, Northern Nut Growers' Association.
Romig (probably *H. ovata*).	Romig Bros., Downington, Pa	An excellent nut.
Sande (probably *H. ovata*).	Elmer T. Sande, Story City, Iowa	One of best known in Iowa.
Swaim (probably *H. ovata*).	H. H. Swaim & Son, South Bend, Ind	Highly prolific.
Vest (probably *H. ovata*).	Luther W. Vest, Blacksburg, Va	Extremely thin shell.
Whitney (probably *H. ovata*).	W. O. Whitney, Berea, Ohio	First prize, 1934 contest, Ohio.
Wilcox (probably *H. ovata*).	P. E. Wilcox, Geneva, Ohio	Second prize, 1934 contest, Ohio.
Hicoria pecan:		
Southeastern region:		
Brake	William H. Brake, Rocky Mount, N. C.	Outstanding cracking and kernel quality.
Brooks	B. W. Stone, Thomasville, Ga	Scab-resistant; prolific; superior cracking quality.
Candy	Theodore Bechtel,[1] Ocean Springs, Miss.	Superior table variety; roundish.
Curtis	J. B. Curtis,[1] Orange Heights, Fla	Scab-resistant; superior cracking and kernel quality.
Desirable	C. Forkert,[1] Ocean Springs, Miss	Large size; scab-resistant; good cracking quality.
Lewis	F. H. Lewis,[1] Pascagoula, Miss	Do.
Mobile	B. W. Stone, Thomasville, Ga.	Prolific; scab-resistant.
Moneymaker	S. H. James,[1] Mound, La	Prolific; early to mature.
Moore	Several nurserymen, Monticello, Fla	Prolific; scab-resistant; early; good cracking quality.
Nelson	William Nelson,[1] New Orleans, La	Prolific; vigorous; scab-resistant.
Russell	H. F. Russell,[1] Ocean Springs, Miss	Scab-resistant; very thin shell; sweet.
Schley	A. G. Delmas,[1] Pascagoula, Miss	Thin shell; very superior kernel quality.
Stuart	W. R. Stuart,[1] Ocean Springs, Miss	Scab-resistant; of good commercial size.
Success	Theodore Bechtel,[1] Ocean Springs, Miss.	One of the best when good; variable.
Southwestern region:		
Burkett	J. H. Burkett, Clyde, Tex	Very fine table variety.
Clark	William Millican, Bend, Tex	Very fine all-around variety.
Halbert	H. A. Halbert,[1] Coleman, Tex	Extremely precocious and prolific.
Nugget	J. A. Evans, Arlington, Tex	Superior shelling quality.
San Saba Improved.	E. E. Risien & Son, San Saba, Tex	Notably thin shell.
Sovereign	do	Notably prolific.
Squirrel	do	Notable flavor.
Supreme	do	Generally very fine variety.
Western	do	Do.
Northern region:		
Busseron	Long a standard; from near Vincennes, Ind.	Matures early; no other advantage.
Clarksville	Arthur L. Norton, Clarksville, Mo	One of the most northern in origin.
Dewitt	George F. Dewitt, Butler, Mo	Superb cracker; high percentage kernel.
Duley	John Duley, New Haven, Ill	Very good all-around nut.
Elmer	Snyder Bros., Inc., Center Point, Iowa.	Should be one of the most hardy.
Fisher	Joseph Gerardi, O'Fallon, Ill	Said to be unusually prolific.
Gallatin	C. W. Richardson, New Haven, Ill	One of the most promising new varieties.
Goforth	Bert Goforth, New Haven, Ill	First prize, 1934 contest, Northern Nut Growers' Association.
Greenriver	Standard variety; Daviess County, Ky.	Best of older northern varieties.
Harmon	Anna S. Harmon, Mount Carmel, Ill.	An excellent seedling, not yet propagated.

[1] Deceased.

TABLE 3.—*Varieties of nuts of probable value for breeding*—Continued

Genus, species, variety, and region	Origin or introducer	Comments
Hicoria pecan—Contd. Northern region—Continued.		
Hofmann	O. J. Hofmann, Henderson, Ky	An excellent seedling, not yet propagated.
Indiana	Long a standard; 300 yards from original Busseron.	Matures early; no other advantage.
Kentucky	Long a standard; northern Kentucky	Excellent midseason pollinizer.
Major	Long a standard; Daviess County, Ky	Excellent nut, but too small and round.
Meyer	Mrs. Tony Meyer, Brunswick, Mo	Should be hardy well north.
Niblack	M. J. Niblack,[1] Vincennes, Ind	Best cracking quality; very sweet.
Norton	Arthur L. Norton, Clarksville, Mo	Large nut; should be hardy north.
Posey	Long a standard; southwestern Indiana.	Handsome tree; excellent cracker.
September	J. F. Wilkinson, Rockport, Ind	Said to be earliest to mature.
Juglans cinerea:		
Aiken	J. F. Jones Nurseries, Lancaster, Pa	From New Hampshire; small but good cracker.
Alverson	M. E. Alverson, Howard City, Mich	Third prize, 1932 contest, Michigan.
Baker	G. A. Zimmerman, Harrisburg, Pa	From New York; highly promising.
Buckley	Park Buckley, Strawberry Point, Iowa	One of best known in Iowa.
DeVan	F. E. DeVan, Rock Creek, Ohio	Fifth prize, 1929 contest, Northern Nut Growers' Association.
Hostetter	C. F. Hostetter, Bird in Hand, Pa	Third prize, 1929 contest, Northern Nut Growers' Association.
Irvine	L. K. Irvine, Menomonie, Wis	First prize, 1929 contest, Northern Nut Growers' Association.
Kenworthy	John F. Kenworthy, Rockton, Wis	Fourth prize, 1929 contest, Northern Nut Growers' Association.
Lingle	E. J. Lingle, Pittsfield, Pa	Sixth prize, 1929 contest, Northern Nut Growers' Association.
Love	Charles P. Reed, Howell, Mich	One of best known in Michigan.
Luther	F. Luther, Fairgrove, Mich	Second prize, 1932 contest, Michigan.
Mitchell	Claude Mitchell, Scotland, Ontario, Canada.	First prize, 1932 contest, Michigan.
Robinson	Mrs. Ada Robinson, Waterman, Ill	One of best known in Illinois.
Sherwood	Snyder Bros., Inc., Center Point, Iowa	One of best in State.
Smith	Horace T. Smith, Chicopee, Mass	One of best known in Massachusetts.
Thede	M. F. Thede, Wayland, Mich	One of best known in Michigan.
Thill	M. J. Thill, Bloomer, Wis	Second prize, 1929 contest, Northern Nut Growers' Association.
Utterback	W. E. Utterback, Sigourney, Iowa	One of best in State.
Wright	Douglas N. Wright, Colchester, Vt	One of best known in State.
Juglans nigra:		
Adams	R. Adams, Scotts, Mich	Highly rated by U. S. Department of Agriculture and Michigan Agricultural Experiment Station.
Allen	Glenn W. Allen, Middleville, Mich	Do.
Asbury	C. D. Asbury, Augusta, Ky	Third prize, 1926 contest, Northern Nut Growers' Association.
Benton	W. A. Benton, Wassaic, N. Y	Second prize, 1934 contest, New York.
Booth	R. A. Booth, Bonsack, Va	Excellent cracking and kernel qualities.
Brown	Mrs. Willard Brown, Rock Bridge, Ohio.	First prize, 1933 contest, Ohio.
Clark	Frank Clark, Lamoille, Minn	Fourth prize, 1934 contest, Northern Nut Growers' Association.
Cowle	B. A. Cowle, Defiance, Ohio	Third prize, 1933 contest, Ohio.
Creitz	W. A. Creitz, Cambridge City, Ind	Excellent cracking and kernel qualities.
Cresco	W. A. Bents, Cresco, Iowa	Very good nut; very hardy.
Dougherty	L. D. Dougherty, Crane, Mo	Very good nut; best for southern latitudes.
Edgewood	Ben F. Walker, Siloam Springs, Ark	Do.
Edmunds	Lewis Edmunds, Glasgow, Ky	First prize, 1934 contest, Northern Nut Growers' Association.
Edras	Gerald Adams, Moorhead, Iowa	High percentage of excellent kernel.
Franklin	G. A. Zimmerman, Harrisburg, Pa	Good nut; blooms very late.
Freel	Mrs. E. W. Freel, Pleasantville, Iowa	First prize, 1929 contest, Northern Nut Growers' Association.
Grundy	John Rohwer, Grundy Center, Iowa	First prize, Iowa State Fair, 1927.
Hepler	George Y. Hepler, South Bend, Ind	Excellent cracking and kernel qualities.
Impit	J. U. Gellatly, Westbank, British Columbia, Canada.	For consideration in Pacific Northwest.
Janson	W. W. Janson, Jefferson, Ohio	Fourth prize, 1933 contest, Ohio.
Kettler	Fred Kettler, Platteville, Wis	Excellent nut; should be hardy in North.
Knapke	J. J. Knapke, New Weston, Ohio	Excellent nut; high percentage of kernel.
Learn	Dane Learn, Aylmer, Ontario, Canada	Very white kernel; very sweet; hardy.
Lee	R. E. Lee, Troutville, Va	One of best yet found in Virginia.

TABLE 3.—*Varieties of nuts of probable value for breeding*—Continued

Genus, species, variety, and region	Origin or introducer	Comments
Juglans nigra—Contd		
Lionberger	John W Lionberger, Table Rock, Nebr	Best yet found in State, very good nut
Marion	Mrs E W Freel, Pleasantville, Iowa	First prize, 1929 contest, Northern Nut Growers' Association
McMillen	Lowell McMillen, Buchanan, Mich	Excellent cracking and kernel qualities
McPherson	A McPherson, Jr, Caledonia, N Y	Third prize, 1934 contest, New York
Mintle	J R Mintle, Glenwood, Iowa	Unusually fine nut
Monterey	L K Hostetter, Lancaster, Pa	Excellent cracking and kernel qualities
Myers	E R Myers, Bellefontaine, Ohio	Unusually thin shell, very good otherwise
Ohio	J F Jones Nurseries Lancaster, Pa	Standard variety since first propagated in 1915
Patterson	Mrs William Patterson Wever Iowa	Excellent cracking and kernel qualities
Pinecrest	Herbert Miller, Richfield, Pa	Do
Rohwer	John Rohwer, Grundy Center Iowa	Second prize, 1926 contest, Northern Nut Growers' Association
Sifford	C L Sifford, Buchanan, Va	Excellent cracking and kernel qualities
Snyder	C H Snyder, Newfield, N Y	First prize 1934 contest, New York
Sparrow	Harry C Sparrow Lomax Ill	Excellent cracking and kernel qualities
Stabler	Thomas P Littlepage Bowie, Md	Many nuts have single lobes, good cracker
Ten Eyck	J F Jones Lancaster Pa	Unusually thin shell
Thomas	J W Thomas & Sons, King of Prussia, Pa	Has long been the leading standard variety
Throp	Ralph Throp, Greensburg, Ohio	Most or all have single lobes
Tritten	Sam Tritten, Lisbon Ohio	Second prize, 1933 contest, Ohio
Waldsmith	L O Waldsmith, Hartselle, Ala	Best black walnut yet found in Alabama
Wanda	Gerald Adams, Moorhead, Iowa	Excellent cracking and kernel qualities
Wetzel	Annie M Wetzel, New Berlin, Pa	Fourth prize 1929 contest, Northern Nut Growers' Association
Wiard	Everett Wiard, Ypsilanti, Mich	Third prize, 1934 contest, Northern Nut Growers' Association
Wright	Herman Wright, Wolcott, N Y	Fourth prize, 1934 contest, New York
Juglans regia		
Concord	French parentage	Leading favorite in central portions of California, blooms late
Crath Seedlings	Poland	Now being introduced by Paul C Crath, Toronto, Canada, in the hope of finding greater hardiness
Ehrhardt	South America	A heavy bearer of high grade commercial nuts
Eureka	Persia	A leading commercial sort blooms late, nuts well sealed
Franquette	France	Late bloomer leading commercial sort of Pacific Northwest
Payne	do	Very precocious and prolific
Placentia	South America	The leading commercial variety in southern California
Juglans sieboldiana [2]		
Bates (Hn)	J F Jones Nurseries Lancaster, Pa	One of best yet tested
Bourne (Hn)	Fred Bourne, Milford, Mich	Second prize 1932 contest, Michigan
Calendar (Hn)	J U Gellatly, Westbank, British Columbia, Canada	Best variety from Pacific Northwest
Cardinell (S)	Bob Cardinell, East Lansing, Mich	Third prize 1932 contest, Michigan
Caruthers (Hn)	A Caruthers, Ferrell, Va	Best variety from Virginia
English (S)	Harold English, Chatham, Ontario Canada	First prize, 1932 contest, Michigan
Evers (Hn)	A H Evers, Petoskey, Mich	Second prize 1932 contest Michigan
Faust (Hn)	J F Jones Nurseries, Lancaster, Pa	Exceptionally vigorous, good nut, large
Fodermaier (Hn)	John J Fodermaier, Dover Plains N Y	Excellent nut highly promising
King (Hn)	John W Hershey, Downingtown, Pa	Do
Lancaster (Hn)	J F Jones Nurseries, Lancaster, Pa	Standard first variety propagated
Mitchell (Hn)	Claude Mitchell, Scotland, Ontario, Canada	First prize, 1932 contest, Michigan
Stranger (Hn)	J F Jones Nurseries, Lancaster, Pa	Said not to be dichogamous
Wright (Hn)	Ross Pier Wright, Westfield, N Y	Very new, apparently one of the best
Juglans sieboldiana hybrids		
Cording × *J regia*	R Bates, Jackson, S C	Extremely rapid grower
Creitz × *J cinerea*	W A Creitz, Cambridge City, Ind	Prolific, reasonably good
Helmick × *J cinerea*	James K Helmick, Columbus Junction, Iowa	Heavy bearer, quite good

[2] Hn = heartnut, S = Siebold walnut

IMPROVEMENT OF FLOWERS BY BREEDING

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AGRICULTURE is above all things practical, and probably few people would think of it as concerned with the production of sheer beauty. Yet American agriculture has $290,000,000 invested in producing beauty, and it pays to the extent of a gross return of $131,000,000

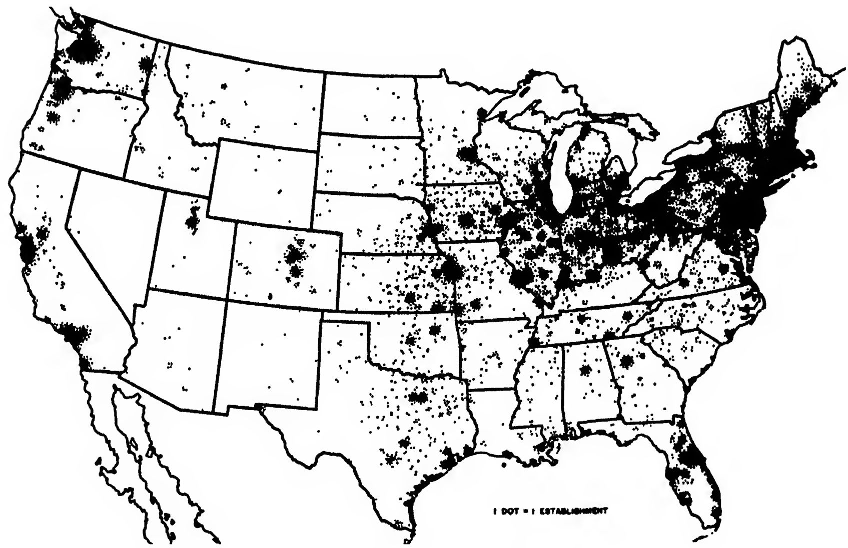

Figure 1.—Approximate location of florists' establishments producing flowers and plants grown under glass and flowers grown in the open, 1929.

a year. These figures apply to the farms and nurseries engaged in growing flowers and ornamental plants, outdoors and under glass.[1] The map (fig. 1) shows both how widespread the industry is and how heavily it is concentrated in certain regions.

This great industry supplies material for the immense number of people who grow flowering and ornamental plants for their own enjoyment. During recent years there has been a rapid increase in the

[1] In 1929, according to the census, there were 13,088 florists producing flowers and plants as a business, both under glass and in the open. The number of commercial nurseries at that time was 7,207, and probably most of these devoted at least part of their space and time to the production of ornamental plants. In addition, 1,935 farms were reported as engaged in growing bulbs commercially. The number of farms engaged in producing seed of flowering plants—a well-developed industry on the Pacific coast, expecially in California—was not included.

planting of flowers around homes and in the planned planting streets, roadways, and parks. The large number of flower shows a exhibits, ranging from the small display of a village garden club the huge annual national and international shows, is one evidence o this interest. In some of these shows the competition for prizes fo new or improved strains or seedlings has become very intense, especially among fanciers of one kind of flower, such as the chrysanthemum, dahlia, gladiolus, rose, or iris.

These demands of both florists and home growers have been the major influence in the development of new and finer types of flowers, and each year there are many new introductions. Undoubtedly changing fashions play a large part in this activity, and the florist must be constantly on the alert to meet them.

BACKGROUND OF FLOWER BREEDING

It is likely that our early ancestors were too busy securing the bare necessities of life to pay much attention to plants that had nothing but their beauty to recommend them. Conscious selection of purely decorative plants probably did not begin until some sort of stable living conditions had been achieved. When early man first began to grow flowers, he very likely transplanted entire clumps from the wild to his dooryard. It is only natural that he should have chosen the best for transplanting and thus practiced the first plant selection in ornamentals. As time went on, the use of flowers and ornamental plants played an ever-increasing part in his everyday life. We know from the remnants of early art that flowers were regarded highly, since so many of them furnished the chief motif in decoration.

The early records of selections and attempts to breed flowering plants are very meager. Considerable work had undoubtedly been done by the beginning of the eighteenth century. The first apparently authentic record of hybridizing flowers, however, appeared in 1717, vhen Thomas Fairchild's cross between a carnation and a sweet-illiam was reported. This occurred during a period when consider-le interest had been aroused by the work of Camerarius, who nonstrated the existence of sex in plants.

he species hybrid produced by Fairchild was completely sterile was commonly referred to as the plant mule. The chief interest e botanists of this period was not so much the production of better s as the accumulation of evidence on sexuality in the plant king- Fairchild's hybrid, however, received considerable attention is described in 1717 in Bradley's New Improvements in Planting rdening, as being neither sweet-william nor carnation, but as ing both equally.

Work of Amateur and Professional Breeders

he existence of sex in plants had be
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flowers. The dev
ng the ninete
work

a back-yard garden. In the numerous organizations interested in some one flower, such as the American Rose Society, the American Iris Society, and others, there are many members engaged in the fascinating hobby of flower breeding. A great deal of this work is never heard of, but undoubtedly it has produced many of our present varieties of such important flowers as iris, gladiolus, dahlia, rose, and narcissus. It involves the making of many thousands of crosses each year in a very wide range of plant material. In an article such as this, it is obviously possible to mention the work of only a few amateur breeders, and this is done here and there under sections dealing with particular plants. It is likewise not possible to discuss all the numerous varieties that have been developed by flower breeders. The following résumé of the number of listed varieties of some of the groups of the commoner flowers is evidence of the extent of interest in this field.

Name	*Number of varieties*
Rose	15,000
Chrysanthemum	1,500
Narcissus	3,000
Tulip	8,000
Sweet pea	500
Snapdragon	400
Aster	600
Dahlia	7,000
Gladiolus	2,500
Iris	4,000
Peony	2,000

Since new varieties are constantly appearing and old ones going out of fashion, the data of this tabulation can be accepted only as approximations. The origin of most varieties of flowers is unknown, and it is beyond the scope of this article to attempt to indicate this for each kind of flowering or ornamental plant, but the named varieties of the plants included in this discussion far exceed in number those of our important food plants. It is safe to say that the productio of such a large number has been possible only because of the work thousands of amateur breeders, whose main compensation has be the pleasure the work has afforded them.

The contributions of the professional breeders, including nurs men, florists, and seedsmen, are likewise very large. It is to work of this group that we owe the development of nearly all modern varieties of such important flowers as the rose, zinnia, pea, carnation, calendula, aster, snapdragon, larkspur, and n tium. While it is true that profit has been a primary factor work, the professional breeder almost always has an inborn l the plants and flowers that are his stock in trade.

all the large flower-seed growers are carrying o ms. Of the many new flowers or so-call each year, some have arisen that occurred in th taneous mutant d or not

instance, to see as many as 5 acres of some one flower, with as many as 430,000 individual plants. This means that the possibility of finding rare multiple recessives is fairly great. Here it is not a question of following the inheritance of one or a few genes. The trained geneticist has an opportunity to find nearly every combination of characters that could possibly arise from the material (fig. 3).

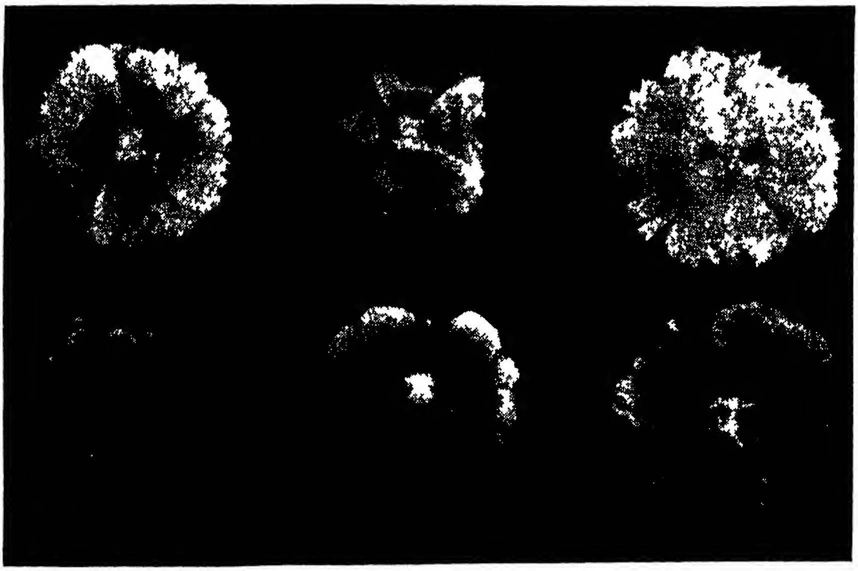

Figure 2.—Variation in hollyhock flowers collected from a group of plants growing in a garden at Davis, Calif. By selection and by controlling pollinations for several years all but the double form could probably be made to breed true. The double shown here is a rather complex form that cannot be bred to come true from seed.

When a new outstanding type appears in a field it is usually recognized. If it seems desirable, a stake is placed beside it and the seed is collected as it matures. In recent years the more careful growers take measures to protect the selected plant against cross-pollination if it is a species not normally self-fertilized (fig. 4). As many as several thousand such field selections may be made each year on a large flower-seed ranch. Only the best variants are carried on, and these are usually not introduced until they breed fairly true to type. While undergoing this period of selection and reselection they are said to be "in the shop" (fig. 5).

There is no doubt that the flower varieties of today are a vast improvement over those of 15 to 20 years ago. Undoubtedly we owe a real debt of gratitude to the amateur and professional breeders whose efforts have made this possible. When it is recalled that most of this work has been accomplished without the aid of a background of knowledge of genetics, the possibilities for the immediate future are indeed bright. In many instances the results could have been accomplished in a much shorter period, and frequently a smaller population of plants would have sufficed. Unfortunately there still

exist many erroneous ideas and beliefs among flower breeders. Some of these will be discussed later in this article.

Need for More Scientific Methods

The accumulation of data and the development of fundamental principles in genetics have gone on at a rapid pace during the last 25 years. As a result there is now available sufficient information prac-

Figure 3.—A field planting in California of annual larkspur for seed. There are several hundred thousand plants in a field of this size. To many the plants would appear uniform, but to a trained investigator there would be countless variants as to flower shape, color shades, plant habit, foliage, and many other characters. (Courtesy of Bodger Seeds, Ltd.)

tically to revolutionize the practices of the average amateur and professional flower breeder. Unfortunately this material is not readily accessible, being widely scattered in scientific journals and papers in many different languages.

Much of the unfamiliarity of flower breeders with this mass of information is probably due to the fact that it has never been called to their attention. For instance, geneticists have known for years that the common flowering stocks (*Matthiola incana* (L.) R. Br.) were limited to a maximum of about 56 percent of doubles and that no more can be obtained; yet considerable money is being spent by florists and seedsmen each year to breed strains that will produce a higher proportion.

No one would think of stepping into an airplane and attempting to fly it without some preliminary instruction, yet apparently nearly

everyone thinks the only requisite for success in flower breeding is a liking for the work. If this article seems to be somewhat more technical than the reader might expect, considering the popular appeal of the subject matter, it is because the authors believe the time has come when those interested in improving flowers must be ready to put some effort on studying the basic elements of their science. Planned breeding is unquestionably a fairly complex job. It does not sit and wait for the "breaks" but goes out and makes them. It has its rules and principles, and he who becomes familiar with them is well repaid in increased efficiency. Some of these rules and principles will be discussed in the following pages.

Figure 4.—A type of bag commonly used to protect selected flower plants from cross-pollination. A stake is driven into the ground close to the plant and a tin or galvanized-iron cylinder open at both ends is placed around the base of the plant and stake. A long cloth bag open at both ends is pulled down over the plant and stake, tied tightly about the metal cylinder, and closed at the top with a drawstring. This gives protection from insect visitors, and if mesh of cloth is fine enough also from wind-blown pollen.

Most of the early technical investigators who worked with flowers were interested mainly in establishing fundamental principles of inheritance. This explains why, until very recently, so few varieties of flowers or ornamentals have been produced by technical workers. Following the rediscovery of Mendel's work in 1900, numerous experiments were carried on to test the validity of his laws. In a goodly share of these, some species of flowering plant was used as experimental material. As a result there was built up a considerable amount of data on the inheritance of many characters in a wide range of flowering plants. This has been summarized and is presented in the appendix of this article.

Recently the possibility of producing strains of flowers resistant to diseases has been receiving more than usual attention. The achievements in this field with some plants such as wheat, sugar beets, cabbage, etc., have stimulated a desire for similar work with flowers. The control of many virus and fungus diseases of flowers is very difficult and offers a challenge to the plant breeder. The success achieved with wilt-resistant asters (fig. 6) and rust-resistant snapdragons is an

indication of the immense possibilities. In this type of work it is very probable that technical workers in public-service institutions will lead the way. A close cooperation between pathologists and geneticists will be essential and is now provided in many experiment stations and in the United States Department of Agriculture. Work in this

Figure 5.—A sweet pea "workshop" in California. Seed from controlled crosses is planted in rows, and when plants are in bloom the breeder takes notes on each lot, selecting the most desirable for further breeding Three long bamboo stakes are placed to form a tripod over each selected plant, and if seed is to be saved a little bag is numbered and tied to the bamboo support. (Courtesy of Ferry-Morse Seed Co.)

field may become involved in difficulties, such as the sudden appearance of other forms of a disease-producing organism that are able to infect hitherto resistant plants. These so-called physiological strains of fungi are discussed at some length in the section on wheat in the 1936 Yearbook of Agriculture. They will be mentioned later under the discussion of rust resistance in snapdragons.

There is also a demand for types better suited to certain unfavorable environmental conditions, such as winter cold, drought, or intense heat. At the present time practically all of the breeding work on flowers is restricted to certain sections of the United States and of Europe. It is very probable that some genetic material discarded as undesirable in one region might be extremely valuable if grown under a different set of environmental conditions. For instance, too glaring

colors would very likely be less intense in a warmer, sunnier climate and the washed-out pink of a hot region is apt to be about right in a cooler habitat. Long, slender, weak stems in a warm section are commonly shorter and sturdier when the plants are grown under cooler conditions.

The effect of length of day on blooming is another very important point that is now given scant consideration by the average flower

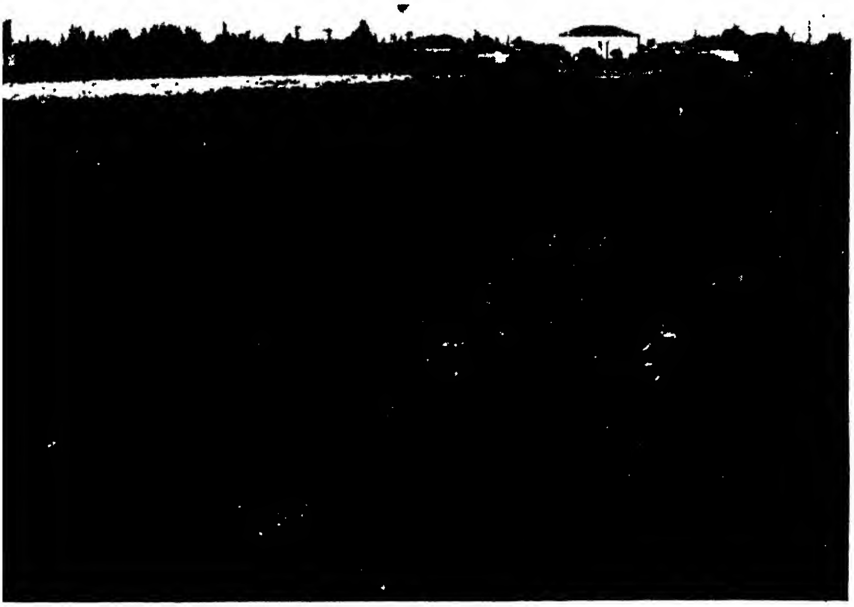

Figure 6.—Wilt-resistant and susceptible asters planted side by side on infested soil. The susceptible plants on the right have been practically wiped out by the disease. (Courtesy of Bodger Seeds, Ltd.)

breeder. When plants of a species known to be sensitive to day length are selected for blooming at some particular time of year in one latitude, it should be remembered that in another their behavior in this respect is likely to be different.

The breeding of winter-hardy perennials is just now beginning to receive some attention. Here also, results will depend to a considerable extent on the location in which the plants are to be grown. Low atmospheric temperatures are less destructive if there is a heavy blanket of snow. This explains why some flowering perennials overwinter nicely in Canada, but are frequently winter-killed in the Ohio Valley.

A very valuable aid in the breeding of flowers is the collecting of new germ plasm by introducing species and varieties native to other parts of the world. This has been done in this country chiefly by the Division of Plant Exploration and Introduction, of this Bureau. The many botanical gardens in all parts of the world also exchange

seeds and plant materials. While some of these introductions are rather unattractive as measured by American standards, yet they may carry very valuable genes. In many instances these "immigrant genes" can be introduced into some of our own standard varieties, giving new and more desirable strains.

As a result of widespread interest and to stimulate greater effort, American seedsmen have established an annual testing of new flowers in what are called the "All-American Trials." New varieties entered by seed growers are planted at a number of locations scattered over the country. A committee of qualified seedsmen in each region observes these plantings and rates each new production on its merits. Awards are then given for the most outstanding introductions. This plan has afforded an excellent stimulus to flower breeding and has probably had much to do with the recent expansion of this work by seed growers.

TECHNIQUE OF BREEDING

The first step in breeding work is the transfer of pollen from the anthers to the stigma of a flower. Two types of pollination are distinguished: self-pollination, when the pollen is produced by the same flower as the seed or by another flower on the same plant; and cross-pollination, when the pollen comes from another plant. Self-pollination is easily accomplished in most cases by enclosing the plant or its flowers in some sort of cloth cage or paper bag so as to protect them from all pollen except their own (fig. 7). Some plants may need a pollinating agent, even though they are fully self-fertile, because the pollen of the flower is shed before its own stigma is receptive, or because the stigma protrudes up above the anthers, or for some other reason. Sometimes such plants merely need to be shaken several times each day in order to scatter the pollen in the bag or cloth cage. Sometimes the best pollination can be secured by the aid of insect visitors, such as flies, bees, or some other species [2] introduced into the cage.

Frequently, however, there is difficulty in getting certain crosses to "take." Sometimes the pollen grain is unable to germinate on the stigma; sometimes it germinates but fails to grow down the style to the egg; sometimes it grows down the style, but the rate of growth is too slow to effect fertilization. Some ingenious devices have been used to overcome these difficulties. When the pollen grains refuse to start growth, they may be germinated in a very weak sugar solution, which is then daubed on the stigma. If the difficulty is due to slow rate of growth, the pollen grains may be placed on the stigma of a young, unopened flower so that they have the advantage of an early start on their journey. If the pollen tubes simply cannot grow down the style tissue, however, there seems to be no remedy, though the same pollen may function normally on the stigma of another closely related plant.

Some investigators have thought that the retardation of growth of pollen tubes was a result of some sort of inhibiting material present either in the style or the ovary of the flower. A Japanese scientist,

[2] See the article on Onion Improvement in this Yearbook for a description of this method.

Yasuda (*558*),[3] became interested in this problem and devised a unique experiment with petunias. In these flowers there occur some self-sterile races. Preliminary work indicated that sterility was due to a slow rate of growth of the pollen tubes. The same pollen applied to other races grew rapidly and effected fertilization. Yasuda conceived the idea of grafting styles from one race of petunias to another. The reader who is familiar with the parts of an average petunia will readily appreciate his difficulties. This very delicate operation was performed with a fairly high degree of success by gluing the grafted style, including its stigma, to the new ovary with a thin layer of gelatine. It was then held in place by being tied, with a thread taken from a spider's web, to a very fine wire support fastened rigidly beside the flower. Since Yasuda wished to determine the source of the material that inhibited the growth of the pollen tubes, he made reciprocal grafts.

Figure 7.—Controlled pollinations of snapdragons. Flowers are enclosed in a glassine bag, and each operation is recorded on attached tag. (From Hilgardia, University of California.)

After the grafts had "taken", pollen was applied to each stigma. On some stigmas the plant's own pollen was applied; on others, pollen from another race. In each instance ungrafted styles were used as checks, some self-pollinated and some crossed. The rate of growth of pollen tubes from the plant's own pollen was more rapid in its own styles when they were grafted on ovaries of another race. Yasuda thought this indicated that an inhibiting substance might originate in the ovary of the flower. Unfortunately, though the rate of pollen-tube growth was given, no statement was made as to whether seed was actually set in ovaries with grafted styles. In this work Yasuda was interested only in the possible presence of the inhibiting material that caused a slow rate of pollen-tube growth.

[3] Italic numbers in parentheses refer to Literature Cited See notice, p 977

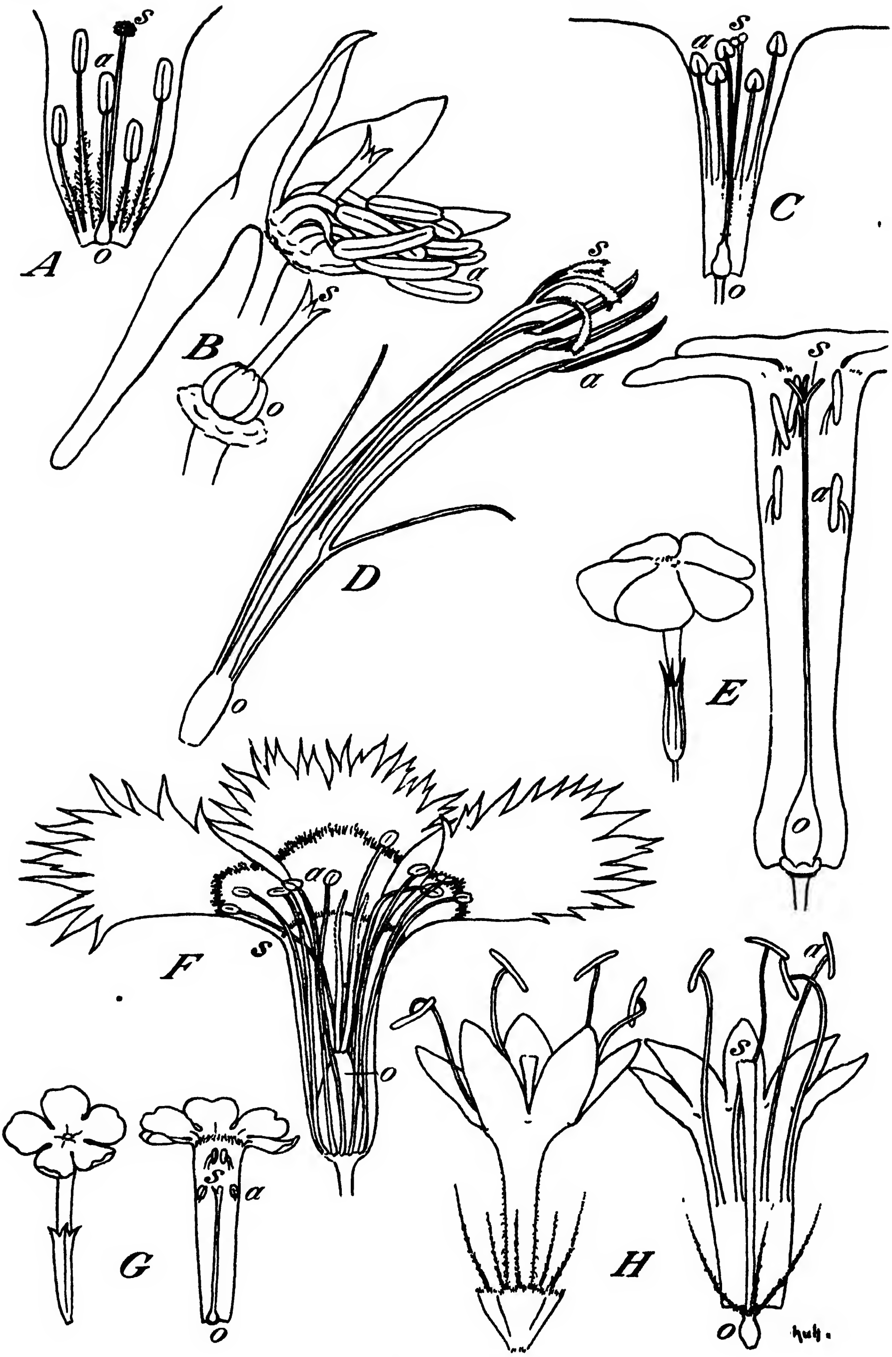

Figure 8.
(Legend on opposite page.)

This same condition of retarded growth rate of pollen tubes is also known in other plants. It has been shown in tobacco and a few others that a series of genes actually control pollen-tube growth, and it is assumed that such genes cause the formation of these inhibiting materials.

The unique method of Yasuda may lead to something valuable in flower breeding. In some cases of cross-pollination where the pollen will not grow in the maternal style it may be possible to secure hybrids by grafting a style from the pollen parent to the seed parent. This, of course, would not work if the inhibiting cause is a substance in the maternal ovary.

Successful cross-pollination depends to a great extent on having a thorough knowledge of the structure of the flower to be pollinated. In some instances it may be so constructed that considerable skill in manipulation is necessary to secure even a low percentage of successful crosses.

When a cross-pollination is to be made it is essential that every precaution be taken to safeguard the stigma from all other pollen. In general this requires the removal of the anthers before pollen is shed. In the case of many members of the composite family, such as marigolds, this is so difficult that another less certain but fairly efficient method is sometimes used. It is based on the structure of the composite floret, in which the style is surrounded by the anthers, which form a closed circle about it. As the style grows it pushes up through the column of anthers, collecting pollen as it goes. The rate of this growth is so rapid in some composite flowers that the stigma emerges from the anthers before the pollen has had time to germinate. If a fine stream of water of moderate force is used promptly, the pollen grains can frequently be washed from the stigma before they germinate.

The structure of some of the commoner flowers is shown in figures 8, 9, and 10. In each instance a longitudinal section is shown in order to bring out clearly the floral parts most important in pollination—the anther, the stigma, and the ovary.

Figure 8 shows some of the flowers in which controlled pollination is most easily effected.

The morning-glory (fig. 8, *A*) is an easy type of flower to emasculate. As shown in the drawing, the style is slightly longer than the stamens. Such a style is said to be exserted beyond the anthers. When a cross-pollination of morning-glories is to be performed, the anthers are removed at any time before they shed their pollen.

The petunia flower shown in figure 8, *C*, is very similar to the morning-glory. There are, however, other flower types in petunia that are more complex. In some of the extreme double types the stamens are greatly reduced or eliminated entirely. Such a flower can be used only as a maternal parent, and crosses are easily made since anthers are not present.

Figure 8.—**Structure of (*A*) morning-glory, (*B*) nasturtium, (*C*) petunia, (*D*) gladiolus, (*E*) phlox, (*F*) carnation, (*G*) verbena, and (*H*) scabiosa to show arrangement of the parts concerned in pollination. The anthers, stigma, and ovary are labeled *a*, *s*, and *o*, and in all instances each flower has been split open and drawn to show the relative position of these three parts. The technique for pollination of each is discussed in the text.**

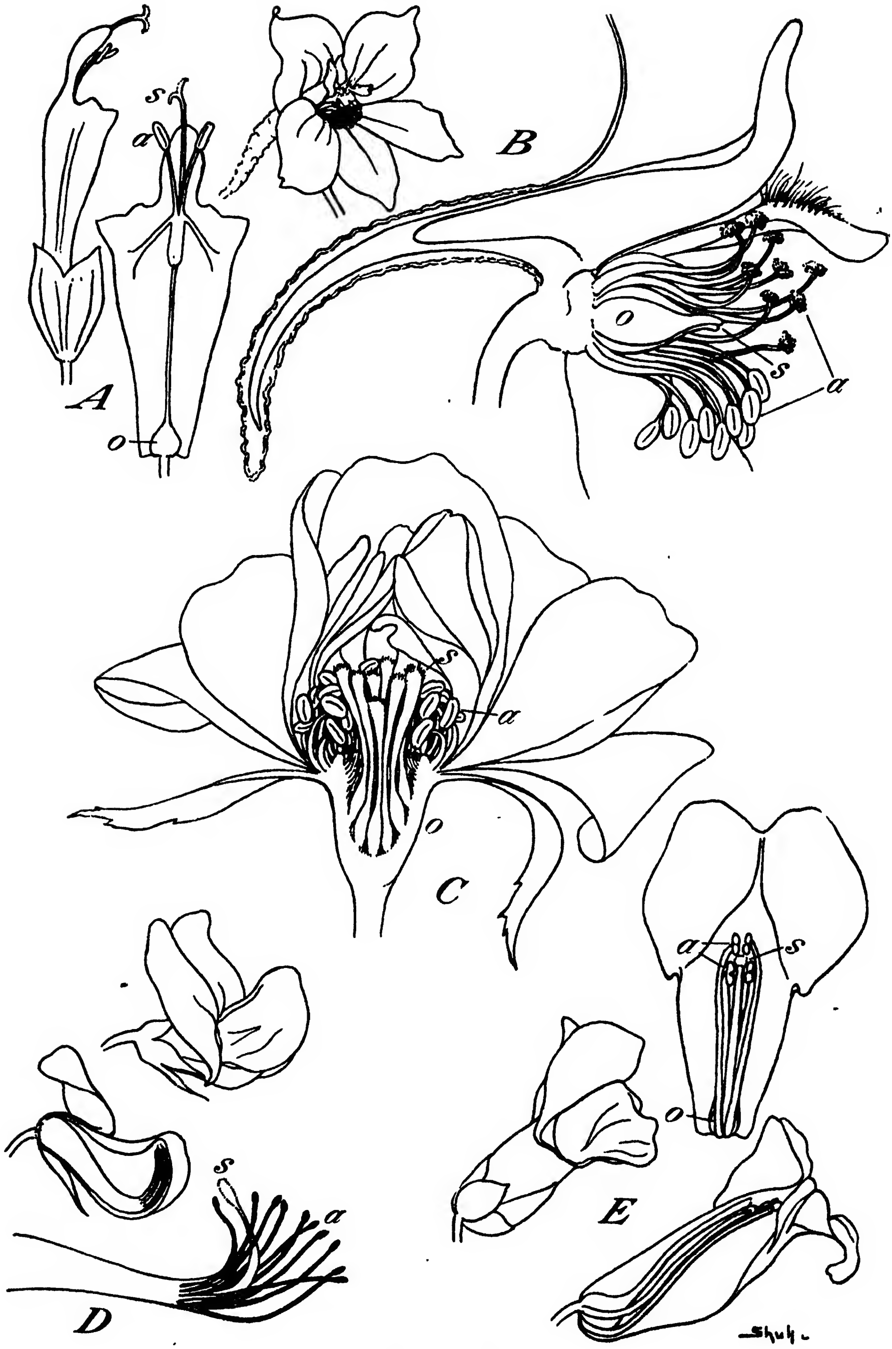

Figure 9.

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In the nasturtium (fig. 8, *B*) the anthers form a tight cluster about the pistil. They are large and may be easily removed before they shed any pollen.

The gladiolus (fig. 8, *D*) has large anthers and a branching, plumelike stigma. Emasculation is very easily accomplished.

Phlox and verbena (fig. 8, *E* and *G*) are very similar in structure, and emasculation is practically identical for both. As can be seen from the illustration, the anthers are fastened to the inside of the tube formed by the petals and may be removed with the corolla, to which they are attached. This should be done just before the small bud opens, shortly after color has appeared in the folded petals. A slight pull at this time brings off the corolla tube with the anthers and leaves the stigma, which may be pollinated when it is receptive.

The carnations or pinks (fig. 8, *F*) also have a wide range of flower types. Only the single form is mentioned here. As can be seen from the figure, removal of the anthers is comparatively simple.

The scabiosa (fig. 8, *H*) is very similar to a composite flower. Here the so-called flower is actually a head of many small florets. In the figure a normal floret and one split open are shown. The anthers protrude so far beyond the stigma that their removal is easily accomplished.

The scarlet sage (fig. 9, *A*) has a rather unusual arrangement of its anthers. As shown in the illustration, they are held out from the flower wall by a bracelike arrangement. The stigma protrudes beyond them.

The larkspur (fig. 9, *B*) has a large number of anthers, which fit very closely about the stigmas of the compound ovary. The anthers may be removed with little injury to the flower, but caution must be exercised to get them all.

Roses vary from the single to the double form. The one shown (fig. 9, *C*) is a double hybrid tea. In emasculating, it is always advisable to clip away as much of the petals as possible. This gives ready access to the anthers, which can then be easily removed.

The sweet pea and the perennial pea are identical as far as emasculation technique is concerned. The sweet pea flower is one of the most difficult to emasculate without causing injury. The anthers, as shown in the perennial pea (fig. 9, *D*) form a closed column around the greater part of the ovary. They then branch out and closely surround the stigma. The removal of this column of anthers frequently injures the ovary, which is tender and brittle. It takes considerable practice to become skillful in the operation.

The snapdragon (fig. 9, *E*) is very easy to emasculate. The anthers do not shed pollen until the flower is fairly large. They may be removed readily without injury to the flower.

In figure 10 several members of the composite family are shown. While all have certain structures in common, there are also some differences that probably warrant a few words of explanation. In this large family of plants, the so-called "flower" is actually a group of

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Figure 9.—Structure of (*A*) scarlet sage, (*B*) larkspur, (*C*) rose, (*D*) perennial pea, and (*E*) snapdragon to show arrangement of the parts concerned in pollination. The anthers, stigmas, and ovary are labeled *a*, *s*, and *o*, and in all instances each flower has been split open and drawn to show the relative position of these three parts. The technique for pollination of each is discussed in the text.

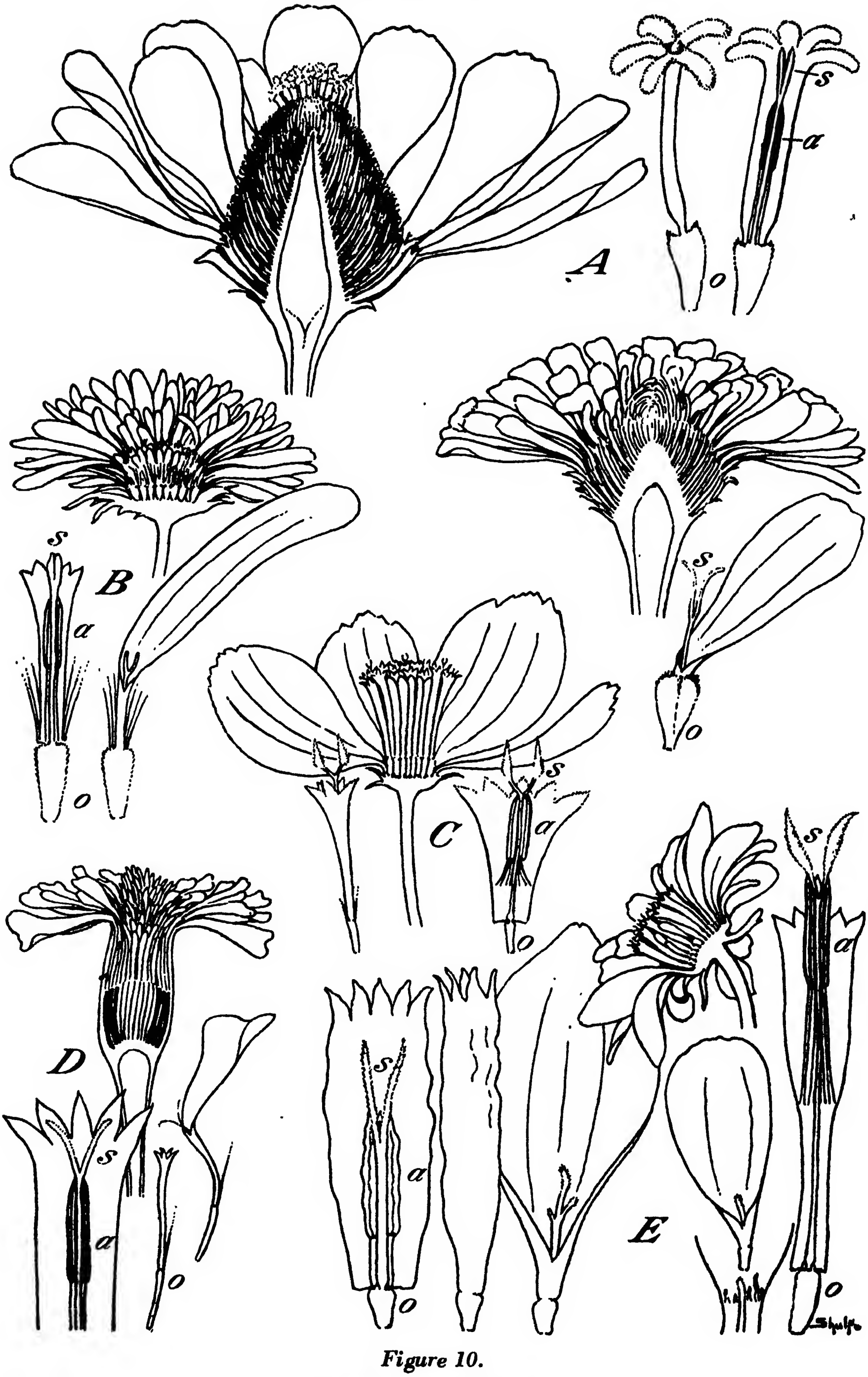

Figure 10.
(Legend on opposite page.)

many small flowers called florets, massed closely together in what is sometimes called a "head." These florets are of two distinct types. Some produce both pollen and ovules and are termed perfect flowers; others lack anthers for pollen production but have pistils for ovule production, and are called pistillate flowers. These small florets may also be classified as to the form of the corolla. In one type the corolla forms an inconspicuous tube surrounding anthers and style. These are found in the center of the head and are called disk florets. In the second type, called the ray floret, the corolla is modified into a conspicuous flat petallike structure, and extends far beyond other parts. The proportion between the two types varies considerably. The doubleness of any composite flower is determined by the number of ray florets. In extremely double flowers in this family, all the florets may be of the ray type.

The zinnia flower (fig. 10, *A*) occurs in at least four types. This information, as yet unpublished, was kindly furnished by C. F. Poole, of the Department. He is continuing his work on zinnias, which he started while a member of the staff of the College of Agriculture of the University of California.

The primitive or wild type is common in practically all races of zinnias. It is called "medicine hat" by seedsmen, and is illustrated at the top left of figure 10. The flower head has a single outer row of ray flowers, all of which are pistillate. The disk flowers are arranged in a somewhat pyramidal form and are all perfect. To the right of the medicine-hat type are shown a single perfect flower and one in which the corolla tube, which is the petal of the floret, has been split to show the anthers and style. Directly below this is shown a flower head of a second type, extremely double. Here all the florets are pistillate (female) and no pollen is found in the entire head. A single floret is shown below it in which the absence of anthers is conspicuous. Between these extremes are two intermediate types. One, more like the medicine hat, has several rows of pistillate florets and fewer perfect flowers. The second has a further reduction of perfect florets and more closely resembles the very double, purely pistillate flower head. Flower growers are interested chiefly in the more double types. These can set seed only if pollinated by some other type. A plant bearing only pistillate florets will certainly not set seed if it is grown under a cage or otherwise isolated from sources of pollen. This is probably the real explanation for some of the self-sterility in zinnias reported by some seedsmen when single plants were grown under cages. Sometimes more than one type of flower head is found on a plant. This condition has not been investigated.

From the above description it will be seen that cross-pollination in zinnias may be done without resorting to emasculation. If sterility factors are not present it is only necessary to make sure of the source of the pollen that reaches the stigmas of pistillate florets. In some

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Figure 10.—Structure of (*A*) zinnia, (*B*) aster, (*C*) cosmos, (*D*) marigold, and (*E*) dahlia to show arrangement of the parts concerned in pollination. The anthers, stigma, and ovary are labeled *a*, *s*, and *o*, and in all instances each flower has been split open and drawn to show the relative position of these three parts. The technique for pollination of each is discussed in the text.

cases this may require the cutting away of perfect disk flowers, but in the purely pistillate double flowers no anthers are present and so no preliminary work is necessary.

As far as could be determined there is no report of any cross-breeding in the China-aster. It is likely that cross-pollinations have been made by amateurs and seedsmen, but no record of this has been available. A careful study of aster flower types (fig. 10, *B*) similar to that of the zinnia has apparently not been made. The aster flower head shown in the figure has both pistillate ray florets and perfect disk florets, and their proportion is a measure of the doubleness of the flower. If there is no complication from sterility, it should be fairly simple to control pollination. Small, curved, sharp scissors could be used to cut out all the perfect florets, and the remaining pistillate ones could then be pollinated as desired.

There is also a wide range of flower types in cosmos. The one illustrated (fig. 10, *C*) is a "single" type. All the florets are perfect, so that cross-pollination would here entail emasculation or removal of the anthers. Cross-pollination might also be done after using a stream of water to wash off all pollen after the two-parted, feathery stigmas have pushed their way through the anthers. If removal of the anthers is necessary, an excellent tool can be made by hammering flat the head of a pin, which is then bent and inserted in the end of a small wooden handle. By careful manipulation the corolla tube with anthers attached can be cut away. Unless considerable skill is attained, this operation will have a high mortality rate among the flowers on which it is used.

The marigold flower shown in figure 10, *D*, is very similar to the aster. There is, however, a wide range of flower types in marigold, as in nearly all other composites. In this flower there are several outer rows of pistillate florets, and those in the center disk are all perfect. The two types of florets are shown below the flower head with a perfect floret split open at the lower left to show anthers and stigma. Cross-pollination in this flower is essentially the same as in the aster.

In the dahlia (fig. 10, *E*) there is a range of flower types from the ordinary single to the complete double. In the single type the flower head is practically the same as the medicine-hat zinnia. In the outer row the florets are pistillate; the disk flowers are perfect. From this all gradations exist up to the fully double type, in which practically all the florets are pistillate. Since these pistillate florets do not produce pollen, few seeds are produced by the large double-flowered dahlias.

The flower shown here is an intermediate double type. To the left is a perfect disk flower as it looks when removed and split open to show style, stigma, and anthers. Self-sterility is the rule in garden dahlias. This makes crossing very simple, since emasculation is not necessary.

There are several precautions to follow in emasculating all flowers. The forceps or other tool used should be kept absolutely clean so that no pollen is carried from plant to plant. This can be done by holding it in alcohol for a minute or so before moving to the next flower. It is also necessary to keep the emasculated flower protected from any chance pollen. This is readily done by covering it with a bag until after the controlled cross-pollination has been made and fertilization has taken place.

The time to apply pollen is also sometimes a problem. In general, it should be done just as soon as the sticky fluid that develops on the

stigma makes it appear moist and shiny. This fluid holds the pollen grains and is nutritive material favorable to their germination.

Methods of Producing Superior Types of Flowers

The earliest and most commonly used method for breeding flowers is known as mass selection. It consists simply in saving for seed only the best plants of a variety. The procedure does not take into account the fact that better plants may be the result of either a better environment or a superior germ plasm. Since the seed from all the selected plants are mixed together before planting, it is difficult to evaluate any progress made. The method also does not differentiate between plants that are highly cross-pollinated and those normally self-pollinated; it is concerned only with the seed-bearing (maternal) parent. Most of our present flower varieties probably were developed in this way.

Mass Selection and Line Breeding

Mass selection does result in a gradual improvement even if some of the selected plants transmit poor germ plasm to the next generation, since the good ones have a better chance to be selected and in time predominate, gradually building up the variety. In this way desirable results are often secured, but frequently many years are required before the effects are noticeable. It is not true, however, even though commonly believed, that the selection process in itself is responsible for the gradual changing or improvement of a flower. There is little reason, in the light of our present information on plant breeding, to continue using this method. But even today it is the general practice among many flower breeders.

Following mass selection came so-called line-breeding. Here the breeder selected single plants and grew the seedlings from each selection separately. In this way the descendants of an individual plant could be studied, and the method was soon recognized as a considerable improvement over the earlier practice. It was possible to determine more readily whether an observed variation was hereditary (in the germ plasm) or simply an environmental modification. It also disclosed the status of a given characteristic in the heredity of a plant. If all the seedlings possessed the characteristic, it might be assumed that the plant was "pure" or homozygous for that characteristic and that it would be passed on to all the descendants; if some seedlings had it and some did not, the plant was heterozygous or mixed in its inheritance.

Unfortunately much of the single-plant-selection work of both amateur and professional flower breeders is done with open-pollinated plants—that is, no provision is made to protect from cross-pollination with other nearby plants. Of course, if a flower is normally self-pollinated, it may not be necessary to have this protection, but there are not many flowering plants that are entirely self-pollinated. The outstanding one supposed to be self-pollinated is the sweet pea. Here the stigma, completely surrounded by a group of anthers, is enclosed in that portion of the flower called the keel (fig. 9, *D*). When the flower matures the pollen is shed and falls on the stigma, which normally does not protrude from the petals forming the keel. In this manner the flower is supposedly protected from all pollen except its own.

Yet conditions in sweet-pea seed fields make this doubtful. If the sweet pea is entirely self-pollinated, it should be a simple matter to keep varieties pure (homozygous), since they could only acquire new genes by way of mutations. While the mutation rate in sweet peas has not been studied, the very large number of offtype plants (rogues) in sweet-pea seed fields certainly cannot be explained on this basis. In some instances these rogues are simply the result of accidental seed mixing, but this is not likely to occur in the case of the more careful growers, who keep their stock seeds separate. Very frequently, also, sweet-pea breeders encounter considerable difficulty in making a strain pure. An examination of several such cases showed that many of the flowers were not fully protected from cross-pollination, as had been assumed. The keel was not fully developed and was too short for the pistil and anthers. As a result the stigma very frequently protruded, even beyond the anthers, so that cross-pollination could easily have occurred.

There are some flowers in which the single-plant-selection method, depending on self-pollination, cannot be used. This may be due to self-sterility, as in some lily species, especially most forms of *Lilium longiflorum* Thunb., and in some iris, petunia, and *Nicotiana* species. Sometimes reasons other than self-sterility are responsible for failure of flowers to set seed when single plants are isolated. The pollen may be discharged before the stigma is receptive, or the reverse condition may occur. The structure of the flower may be such that self-pollination is impossible without the aid of some agency such as insects. Sometimes, as in species of *Lychnis*, the plants are either male (staminate) or female (pistillate). Such types obviously cannot be self-pollinated.

Single-plant selection or line breeding has many advantages over mass selections. When accompanied with self-pollination it quickly gives strains very uniform for habit of growth and other characters. All undesirable qualities are disclosed rapidly and may be eliminated within a comparatively few generations. Unfortunately, continued self-pollination frequently results in a loss of vigor. As a rule this weakened condition may be corrected by making cross-pollinations between inbred strains. This situation has received considerable attention from corn breeders and is discussed at some length in the 1936 Yearbook of Agriculture.

Hybridization

A third method of flower breeding is the making of crosses between plants to secure new individuals that combine desirable qualities from each parent. While it is true that many of the early workers did cross-pollinate flowers, few realized the necessity of carrying their work beyond the first hybrid generation, called the F_1. In other words, if none of the hybrids was desirable, all were discarded.

The rediscovery of Mendel's work in 1900 demonstrated at once the importance of continuing into subsequent generations. Mendel showed that when two plants are crossed, each contributes to the heredity of the resulting hybrid. While ordinarily these contributions are exactly equal in quantity, they may vary qualitatively. When the two bits of heredity-carrying protoplasm, male and female,

are united in one individual, the hybrid, new combinations of characters become possible in the descendants of this hybrid. These new combinations may not be seen in the hybrid, but they will appear in some plants of the population descending from it.

Unfortunately, Mendel's basic laws are still unknown to many flower breeders. Each year many thousands of hybrid seedlings are undoubtedly grown and discarded as being inferior. If many of these had been carried into the next generation, it is likely that some worthwhile plants would have appeared. It is this second generation, commonly called the F_2, in which recombinations of parental characters are found.

In some instances the hybrid between two flowers is self-sterile. This commonly occurs when the two parents are from different species. Although the hybrid sets no seed with its own pollen, some seed may often be secured by crossing it with one or both of its parents. This is commonly called backcrossing. A backcross may be made in both directions; that is, the hybrid may be crossed to the maternal or the paternal parent. Sometimes a backcross will produce fertile seed in only one way, and as a rule it is more often successful when the hybrid is used as the maternal parent.

The method of improvement by hybridization will undoubtedly play an increasing role in flower breeding. It is the only way by which new combinations of desirable germ plasm can be effected. Very frequently a variety may be desirable in many ways, yet have some one characteristic that causes it to be unpopular. In many cases this character can be replaced by a desirable one from some other variety. A cross between them will provide an opportunity to combine the desirable traits of both parents in the F_2 or later generations. Some of the characters of one parent may be recessives, in which case they will not be apparent in the hybrid, but they will appear in some members of the next generation. Here, too, will be found the recombinations, that is, the new plants produced by combinations of characters from each parent. But since the genes, or carriers of heredity, are in the chromosomes, and all the genes in the same chromosome tend to be inherited together (this is the phenomenon known as linkage), we may find undesirable qualities associated with the ones we want. When this occurs it is necessary to grow populations large enough to get a reassortment of the genes or characters, which is brought about by what is called crossing-over, or the occasional exchange of material between chromosomes when the pollen grains and egg cells are being formed.

The backcross procedure mentioned above is probably one of the most valuable methods the flower breeder can use, and it should be more widely employed by amateurs and professionals. When two plants are crossed, usually the breeder has in mind some ideal type that he hopes to fashion by combining many desirable characters from one parent with fewer characters of the other. When this is true, it is best as a rule to backcross the hybrid to the more desirable parent. The resulting offspring may be again backcrossed one or more times and then self-pollinated. In a few generations the chances are that the desired inheritance of the best parent will be piled up and by selection the desirable characters of the other parent can be

retained so that plants closely approximating the ideal will be secured. The chief merit of this method is in recovering the quantitative characters of one parent from comparatively small populations in a relatively short time.

Mutations

In addition to the breeding methods already discussed, many varieties of flowers originate as mutations or sports. Mutations may arise in the pollen grains or in the egg cells, or they may occur in cells of the stems, leaves, flowers, or other portions of the plant. Many of our varieties of roses, carnations, and chrysanthemums have appeared in this way. Sometimes a side branch bears a flower differing in color or size from the remainder of the parent plant. When the plant can be propagated vegetatively, it is usually a simple matter to introduce the changed form or mutant as a new variety. For some as yet unknown reason, certain varieties of some flowers are especially noted for the number of bud sports they have produced. This is particularly true of the Ophelia rose. Many of the present-day varieties of greenhouse carnations are also mutations of this sort.

When a mutation occurs in a sex cell it does not appear until the next generation. If it is a recessive and the parent plant normally is cross-pollinated it may not show up for several generations. It is entirely probable that some of the new characters that appear in a variety of flowers grown from seed arise as sex-cell mutations. The vast majority of the so-called "breaks", however, are not mutations but simply recombinations of already existing characters following cross-fertilization (fig. 11).

Since the chromosomes are the carriers of the hereditary units, any changes in them should have an effect on the plant. Such a change may effect a rearrangement of the genes in a single chromosome or even the loss of some of them. Sometimes a whole chromosome is lost or an extra one added, or each chromosome is reduplicated so that the entire number is doubled. Occasionally one may be broken and the fragment retained or lost. The plant that results from any of these changes is likely to be different from one with normal chromosomes.

The doubling of the chromosome number may occur in several ways. The sex cells sometimes form with all the chromosomes present rather than half the number, which is normal for sex cells. In other instances an ordinary cell in a stem or root may double up its chromosome number, and then when this doubled cell divides all its descendants will have the doubled number.

A well-known example of the doubling of the chromosome number in stem cells is the case of *Primula kewensis* W. Wats. (Kew primrose), as reported by Digby (*111*) in 1912, and by Newton and Pellew (*390*) in 1929 (fig. 12). It is a desirable primula, now quite commonly grown by many florists. It originated in this manner: A cross was made between the species *P. floribunda* Wall. (buttercup primrose) and *P. verticillata* Forsk. (Arabian primrose). The hybrid was completely sterile for many years, when there suddenly appeared on one plant a branch that bore large fertile flowers. The chromosome number of both *floribunda* and *verticillata* is 18, and that of the large-flowered branch was 36. Undoubtedly this branch arose from a cell that had doubled its chromosome number.

Another interesting instance of the origin of a large-flowered plant as a result of chromosome doubling was reported in *Campanula persicifolia* L. (peachleaf bellflower) by Gairdner in 1926 The normal species has 16 chromosomes, and from it came a seedling with 32 chromosomes. The doubling of the chromosome number resulted in a considerable increase in size, and the new variety was named Telham Beauty.

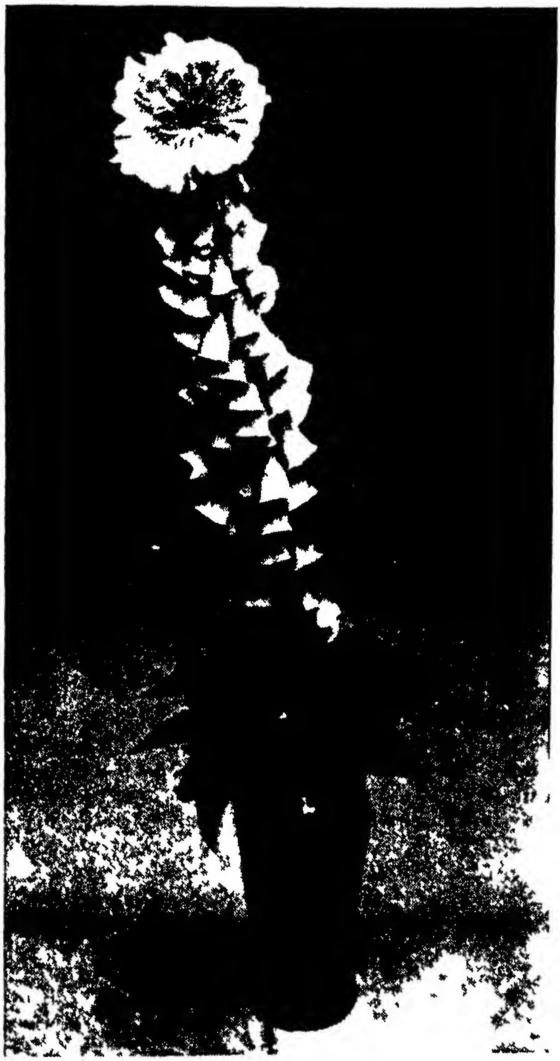

Figure 11.—A horticultural form of foxglove in which the top flowers are united to form a round, hollyhocklike flower. This photograph was sent to the senior author as representing a possible new mutation supposedly arising spontaneously in a home flower garden. It is a form that is not widely distributed but has been known for a long time. It is recessive, so that when crossed with "normal" all the hybrids are normal and the next generation is composed of 3 normal to 1 abnormal.

Quite recently, Randolph (*423*), of the Bureau of Plant Industry, in cooperation with Cornell University, has developed a method by which chromosome numbers of corn may be doubled. While no report has as yet appeared concerning its use for doubling chromosome numbers of flowers, it seems likely to play an important role in future flower breeding The results are secured by the application of heat to the flower just after fertilization has taken place The time between application of pollen to a stigma and the actual union of the two sex cells is very variable It may require only a few hours or it may take several days. The new cell formed by the union of the two is the first cell of the young embryo. This one-celled embryo usually does not divide for some time, and it is during this

period just at or before division that heat is applied. Since the temperature necessary is very likely to be different with different plants, it can be seen that a considerable amount of preliminary investigation will be needed before this method can be used with certainty.

There are on record several cases of spontaneous doubling of the chromosomes in the one-celled embryo. The one of interest here, because the parents, commonly called flowering tobaccos, are frequently found in flower gardens, is that of *Nicotiana digluta* Clausen and Goodspeed. Clausen and Goodspeed (*76*) reported a plant with 72 chromosomes coming from a cross between *N. glutinosa* L. with 24 chromosomes and *N. tabacum* var. *purpurea* with 48 chromosomes. All the hybrids should have had 36 chromosomes, but this one plant had 72. They believed that this particular F_1 plant had doubled its chromosome number shortly after fertilization. There is also evidence of a similar occurrence in tomatoes. In general the doubling of the chromosome number is usually accompanied by an increase in the size of the plant and flower.

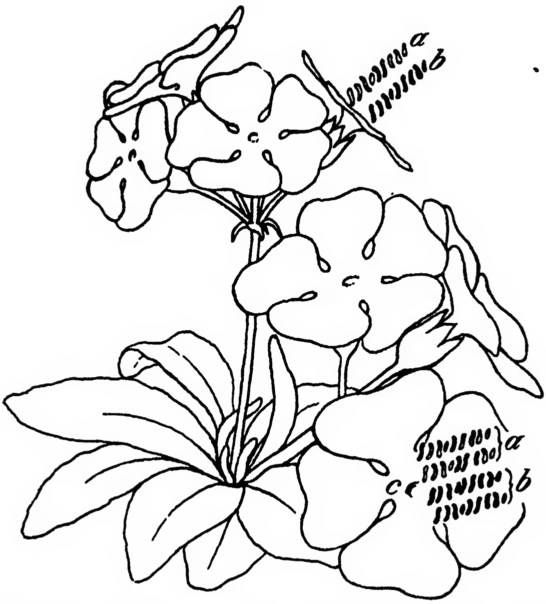

Figure 12.—Diagrammatic drawing showing the effect of the doubling of the chromosome number in a species hybrid. The plant is a cross between (*a*) the Arabian primrose (*Primula verticillata*) and (*b*) the buttercup primrose (*P. floribunda*). It has 18 chromosomes, like each of its parents (the chromosomes are represented near one of the upper flowers). Suddenly it produced the lower branch with larger flowers, and this was found to have 36 chromosomes (represented on one of the petals). Whereas the hybrid itself was sterile and set no seed, the new branch with 36 chromosomes was fertile and set seed. This fertile side branch was the progenitor (*c*) of the well-known Kew primrose (*P. kewensis*).

Chromosomes may also be modified in structure. The modification may result from the breaking of a chromosome into several parts, or from a slight change in one of the genes that it carries. There are many recorded instances of such changes occurring in nature. Frequently they cause freakish and abnormal plants, but they are also responsible for many worth-while new variations. Until recently these changes were purely chance occurrences over which the breeder had no control. Recently, however, certain external agents such as X-rays, radium, ultraviolet light, heat, and some chemicals have been shown to be effective in producing them.

Artificial Methods of Changing Germ Plasm

The use of X-rays, radium, and ultraviolet light for the production of new flower types will probably not become general. Considerable danger is involved, and the work should be done only by thoroughly trained technicians. The actual manner in which these agencies cause the chromosome to change is not known, but the very short rays seem to incite rearrangement of genes and even chromosome breaking.

Some of the earlier work showing the effect of X-rays and radium on flowers was done by T H. Goodspeed (fig. 13) and his associates at the University of California. The plants were several species of ornamental tobaccos. Both seeds and sex cells were exposed to the action of radium and X-rays. In the case of ungerminated seeds there followed a very noticeable retarding of germination, but at maturity no general effect of X-radiation of the seeds could be seen. If, however, the seed was germinating or if tiny seedlings were X-rayed, many changes in growth and form were noticed.

Figure 13.—T. H Goodspeed, professor of botany, and director, Botanical Garden, University of California, Berkeley. One of the pioneers in the use of X-rays and radium to induce mutation in plants.

In another series of experiments by Goodspeed and Avery (*145*), sex cells were exposed to X-rays. This was done by X-raying buds in which the egg mother cells were just beginning to go through the series of divisions that give rise to the egg cells or female gametes. After this treatment these buds were pollinated with pollen from untreated flowers. Now if a change occurred in an egg cell and this egg cell was pollinated by normal pollen, the new condition would show up at once if it was a dominant. If the new character was recessive, however, it would not appear until the next generation.

Following this treatment many plants were secured that differed markedly from their sister untreated plants. One of these variant plants was selected for further study and was self-pollinated. After six generations, that is, six cycles "from seed to seed", seven pure-breeding new types and seven not yet fixed have been secured. Some of these new types differ so markedly from their un-X-rayed sister plant that they probably are entirely new varieties, and even in a few instances new species. They differ from one another and from the untreated plant in habit of growth, in form of leaf, flower, and capsule, and even in the color of leaf and flower.

This series of experiments is remarkable in several respects. It is the first to demonstrate the possibility of actually securing fertile new

types of flowers by X-raying sex cells. All 14 types came from a single X-rayed egg cell, which was pollinated by an untreated pollen grain.

Recently there has appeared another report of effects of X-raying a flowering plant. In the laboratory of the General Electric Co. at Schenectady, N. Y., Moore (*374*) exposed Regal lily bulbs to X-rays. Among those so treated, two upon blooming showed an unusual behavior of the anthers. The flowers differed only slightly from the normal Regal, but the anthers did not open and shed their pollen. Since the pollen is considered unsightly when scattered on the petals, this nonshedding habit is considered by the originator as valuable. These plants are easily propagated by divisions of the old bulb so that they can be multiplied without recourse to seed and also with the certainty they will all be identical, unless there is a reversion to the normal.

Another series of interesting experiments with X-rays was conducted by Morgan (*377*), who exposed seeds, flower buds, and corms of freesias to various dosages. Very little effect was noticed on seed and flowers except when exposures were strong and for rather long periods. The corms, however, showed decided effects from the rays. The untreated corms produced single plants, while as many as five "shoots" were produced by a single X-rayed one. The treated corms also started to germinate immediately after planting, made more rapid progress, and showed curling and twisting of leaves and stems; and the flowers were split and deformed. In general, the effect of X-ray treatment in low dosage seemed to be an acceleration in the rate of growth and the stimulation into growth of structures that otherwise would have remained latent. With increase in intensity of the dosage, the acceleration was lost and the rate of growth was even retarded. The heaviest dosages killed the corms.

In another similar series of experiments, tulip bulbs were exposed to X-rays by Van Heijningen and his associates (*197*) at the Wageningen station in the Netherlands. In many instances the results parallel those with the freesia corms. After moderately strong exposures, the number of small increase tulip bulbs was slightly more than in untreated bulbs. The flowers produced by the treated bulbs in some cases had irregular incisions on the petals, quite similar to those in the so-called Parrot varieties.

Not much in the way of practical results has been accomplished as yet by using artificial physical methods to induce changes in the germ plasm. This is not surprising, however, when it is remembered that although earlier sporadic attempts had been made, less than 10 years have passed since the present type of research was started. Much of the recent and current work of this type with flowers and other plants is still in the experimental stage. Enough has been done to indicate that plants, and even parts of the same plant, differ in response to the same dosages of rays. This means that much preliminary work is necessary merely to discover what dosages to use. There has also been too great a tendency for some to rush into the work while lacking a proper background in genetics and plant breeding. Instances are known in which seeds or pollen have been X-rayed, and when nothing unusual appeared in the resulting plants the entire

lot was discarded. If any recessive changes in the germ plasm were effected, they might not appear until later generations. In this connection it is recalled that Goodspeed continued his work into many succeeding generations and located numerous definite new types. In much of the work also, the number of treated individuals is very small. If the frequency rate of valuable changes is but 2 or 3 in 1,000, there will be little chance of securing them when only 10 to 20 seeds or plants are treated.

WHAT THE STUDY OF CELLS CONTRIBUTES TO FLOWER BREEDING

THE trained breeder likes to know the number of chromosomes in the plant with which he is working. For one thing, it determines the number of individual plants he will have to grow to get a desired recombination of the characters in which he is interested. Suppose, to take a purely imaginary case, that a certain plant has oblong red petals. The breeder wants to get a hybrid with the red color, but does not want the oblong shape. Now if this plant has four chromosomes in its sex cells, the chances are one in four that these two characters are linked—that is, they are in the same chromosome and will usually be passed on together in inheritance. But if there are eight chromosomes, the chances are only one in eight that they will be linked. In the latter case, he has twice as great a chance of getting one character without the other. The smaller the number of chromosomes, the greater the chance of linkage among any two or more characters and the larger the number of individuals that will have to be raised in an attempt to break up the linkage by crossing-over.

Another point of interest to the breeder is the important part that chromosome numbers appear to play in the probability of securing fertile crosses between two species. When both have the same number, the chances for success are much greater than when they differ. There are, however, many instances of hybrids between species with different numbers of chromosomes. As a rule such crosses are more likely to be successful when the one with the greater number of chromosomes is used as the maternal parent. There are, however, a few instances where crosses have been successful even when the species with fewer chromosomes was the maternal parent.

In addition to the question of linkage, the chromosome number may throw light on other questions. For instance, the lilies commonly have 12 chromosomes in their sex cells, which means that they have twice 12 or 24 in their body cells (12 pairs). Now for years the so-called Tiger lily (*Lilium tigrinum* Ker) was noted for its persistent self-sterility. Recently it has been shown to have 36 chromosomes in its body cells instead of 24—3 of each kind instead of 2 of each kind.[4] This is an abnormal condition, but it occurs fairly commonly in plants, and it often accompanies or causes sterility. There are also plants with four times the basic or sex-cell number of chromosomes, or five times, or six times, and even some plants that retain the basic or single number in the body cells instead of doubling this number, which is the normal method. In some species of plants, different

[4] A fertile *tigrinum* has been reported rather recently. According to Stout it varies somewhat from the older common form and apparently has 24 chromosomes rather than 36. It is therefore a diploid.

Figure 14 (legend on opposite page)

varieties run a whole series of these numbers. Thus in the lilies there might be one variety with 12 chromosomes in the body cells (haploids); another with 24 chromosomes (diploids) as shown in figure 14; another with 36 (triploids); another with 48 (tetraploids); another with 60 (pentaploids); another with 72 (hexaploids). Hereafter, these names will be used to indicate the number of times the basic number is multiplied in the body cells of the plant.

Variations in Chromosome Numbers

The question now arises as to how the knowledge that the Tiger lily is a triploid can possibly aid flower breeding. To answer that, it is necessary to give some preliminary discussion. First, it will be remembered that normally the sex cells of a plant always contain half the number of chromosomes in the body cells. This reduction in the number of chromosomes is one of the things that happens when a cell gets ready for reproduction. Now there are many known triploids in plants, and without exception they are all highly self-sterile, but some will set seed when pollinated by a diploid. It is probable that these triploids arise in two ways.

(1) A tetraploid type may be pollinated by a diploid. For instance, in the China-aster the basic or haploid chromosome number is 9, so that a diploid would have 18 chromosomes and a tetraploid 36 in its body cells. When the reproductive cells are formed, these numbers are cut in half; the sex cell of the diploid has 9 chromosomes and that of the tetraploid 18. Now the two sex cells join. Nine chromosomes are added to 18 chromosomes, and the result is 27 chromosomes, or a triploid, since 27 is three times the basic number.

(2) The male or the female nucleus of a normal diploid cell may fail to reduce its chromosome number in preparing for reproduction. In this instance it would keep 18 chromosomes instead of reducing the number to 9. When it united with a normal sex cell having 9 chromosomes the total would be 18 plus 9, or 27—a triploid.

Figure 14.—Chromosomes and formation of pollen grains in the Easter lily as seen under the microscope (× 350). *A*, The cell that will divide twice to form four pollen grains. The chromosomes are all long fine threads and form a tangled knot. *B*, After the first division is well started; the knot has unraveled and the chromosomes are pairing. Since the lily has 24 chromosomes, there should be 12 pairs. *C*, The division has progressed to where 12 pairs of chromosomes can be seen very clearly. *D*, A little later stage of division, in which the chromosomes have become shorter and thicker. The 12 pairs are all clear with the exception of no. 5, which lies under no. 6. *E*, A side view of the 12 pairs just as they are about to separate. *F*, Here 12 chromosomes have moved to each of two sides of the cell and the first division is almost completed. *G*, The 12 chromosomes in each group are now organizing new cells and getting ready to divide again. *H*, There are now 12 chromosomes in each dark-stained nucleus, and each nucleus will again divide to form 4, which finally become pollen grains, each with 12 chromosomes. *I*, Occasionally in the Easter lily something happens that causes the chromosomes to break into many small pieces. Such results can be accomplished by use of X-rays, radium, and possibly heat treatment just before the cells start to divide. *J*, In this cell 11 of the 12 chromosome pairs behaved normally, but two chromosomes probably did not pair. They are the ones at top and bottom. *K*, A giant (tetraploid) cell with 48 chromosomes instead of 24. Such cells are not known to have given rise to any tetraploid lily plant.

Tetraploid lilies are not known to occur, and it is therefore assumed that the triploid form must have arisen in the latter fashion—though there may have been a tetraploid parent that has not been discovered or that has become extinct.

If a triploid is not valuable in itself, there is usually little reason for using it in a breeding program. As a rule, when it is crossed with a diploid, the resulting hybrids are inferior, usually being dwarf, self-sterile forms. If their chromosomes are examined they are found to vary in number from plant to plant. Thus a few successful crosses between the Tiger lily and other lily species have so far given only small deformed seedlings. It has already been noted that the Tiger lily has 36 chromosomes, the other species 24. While no evidence is available as to the chromosome numbers in the hybrids, it is very probable that some had 24, some 25, 26, 27, etc.

As more and more is accomplished in chromosome studies of flowers, it is likely that we shall find other instances similar to the Tiger lily. If a valuable triploid flowering plant appears and can be propagated by cuttings, it is not essential that it be fertile and bear seed. For instance, a valuable triploid carnation, chrysanthemum, rose, narcissus, or geranium could easily be increased by division. With suitable developments in technique it might be possible to create other triploid forms as fine as the Tiger lily.

Other Chromosome Peculiarities

Sometimes a variety persists in producing year after year a number of peculiar variant forms. Even though it is carefully self-pollinated the variant forms may reappear with great regularity. Such a plant cannot be made to breed true, and sometimes the situation is the result of the structure and behavior of its chromosomes. Keeping in mind that the chromosomes carry the hereditary genes it is not strange that these peculiarities of inheritance can be traced to abnormalities in chromosomes.[5] Such plants may show a peculiar behavior of their chromosomes when sex cells are formed, as has been conclusively demonstrated by cytologists working with the evening-primrose.

One of these evening-primroses, known as Lamarck's, produces several variant forms year after year. At first plant breeders thought these were distinct changes in genes in the chromosomes. They were called mutants and the change in the gene was thought to have happened when the sex cells were formed or before. Careful cytological study of chromosomes in the sex cells demonstrated that the evening-primrose chromosomes act very irregularly while pollen grains and egg cells are being formed. These irregularities result in some few sex cells receiving an unusual combination of chromosomes. Since chromosomes are the carriers of hereditary characteristics, such peculiar sex cells naturally give rise to unusual and unexpected seedlings. Unless the sex cells had been examined under the microscope, we would have continued believing that the evening-primrose produced a very large number of mutations. This might have led us into other errors by encouraging the idea that mutations are relatively common. In fact this belief does exist among many amateur and

[5] This statement has some exceptions, chiefly a few instances of cytoplasmic inheritance, dependent on the cell material outside the nucleus.

professional flower breeders. It is expressed in the claim of the sudden appearance of what are commonly called "breaks", which follow the crossing of two varieties. Thus we often see it stated in a popular article that some new flower originated as a break from the hybrid made by crossing two older varieties. It is unquestionable that mutations do occur now and then, but they are comparatively rare. The chances are preponderantly in favor of the breaks actually being recombinations of characters that already existed in the two parents.

A situation that appeared to be somewhat similar to the evening-primrose problem was called to the attention of the senior author of this paper several years ago in California. The late J. H. Franklin, of the Waller-Franklin Seed Co., told of a peculiar breeding behavior in annual larkspur. He had been working for years with a pink-flowered form called Exquisite Pink. The shade of color and the habit of the plant were very desirable, and it was popular with florists. Unfortunately he had not been able to get a pure-breeding strain. Year after year his best selections produced the same variant forms. These undesirable types included a white-flowered form, a rose, a blue, a rose with blue flecks on the petals, a white with blue flecks, and a purplish blue. He sent some seed to the California Agricultural Experiment Station at Davis, where it was grown, and the plants were studied. For 2 years, Exquisite Pink plants were self-pollinated and each time they produced the same variant types. The next year microscopic slides were made of the developing pollen grains, and some of the same general types of irregularities were found that occur in the evening-primrose. Apparently some structural peculiarities in the chromosomes were causing the difficulties. This meant that the Exquisite Pink larkspur could never breed true. When this was explained to Dr. Franklin, the strain was discarded. New selections were started with other pink-flowered forms, and at present there are several good pink larkspurs available.

One of the most popular flowers for both breeding and cytological research is the stock, *Matthiola incana* (L.) R. Br. This plant is unique in that it has two distinctive types, the single- and double-flowered forms, the latter containing no anthers or pistils and making no seed whatever. Reproduction, then, is from seed produced by the single flowered plants. The growers of stocks, both florists and amateurs, are interested almost exclusively in the double forms. For some time plant geneticists have known that there are three types of single plants. One when self-pollinated produces no doubles, the second produces about 25 percent of doubles, and the third from 54 to 56 percent. Obviously the third type is the one to use for seed. It is called ever-sporting because of the high percentage of doubles it produces.

The problem of explaining the peculiar behavior of the ever-sporting stock attracted many workers. One quite logical explanation assumes some condition that kills half the pollen grains and approximately 6 to 8 percent of the egg cells. This might be caused by what is called a lethal gene located in the same chromosome as the gene for singleness. The lethal gene would have to be recessive since if it was dominant all plants with this gene would die. Being recessive a plant can carry the gene and its normal allelomorph and be able to live. Let us use the symbol *a* for the lethal gene and the symbol *A* to represent the normal

allelomorphic gene that is dominant to *a*; then all plants of the *aa* type would die, but *Aa* plants would live.

Now singleness in these stocks is dominant to doubleness. Single-flowered plants may be pure (homozygous) for singleness, or they may be hybrid (heterozygous) for this character. A pure (homozygous) single gives only singles when it is self-pollinated. A heterozygous plant gives 3 singles to 1 double. According to the above theory, the third type, the ever-sporting race, should be hybrid (heterozygous) for singleness and for the linked lethal, which would result in 54 to 56 percent of doubles instead of only 25 percent.

In 1931 Philp and Huskins (*408*) published a cytological study on ever-sporting stocks that apparently explained the situation.[6] In order to understand their work it is necessary to recall that only one of each pair of chromosomes occurs in a sex cell. The pair of chromosomes of which one member carries the gene for doubleness and the other member the gene for singleness, therefore, never get into the same sex cell.[7] Philp and Huskins are able to show that ever-sporting single plants had one pair of chromosomes that differed from one another in appearance, one lacking a small knob on its end. This is very significant when it is remembered that the two chromosomes of a pair normally have an identical shape. From their work, they stated that the pollen grains getting the chromosome lacking the knob did not function. In other words, the absence of the small knob acted as a lethal to the pollen grains in which it occurred.

If only the "double" pollen grains can function, while both "double" and "single" eggs are good, it is easy to see how such plants produce about half doubles and half singles. The fact that the ratio is not exactly 50–50 is explained by assuming that a few egg cells getting the chromosome lacking the knob do not function. This explanation was verified to some extent by a study of pollen germinations from pure and ever-sporting singles, which showed that germination of ever-sporting pollen was only about half that of pollen from pure singles. Evidently about half the pollen grains of an ever-sporting single were being killed in some manner.

The entire situation is much clearer if figure 15 is studied. At the top are shown the seven pairs of chromosomes of a single-flowered ever-sporting stock plant. The members of each chromosome pair look exactly alike with the exception of the first. One lacks the little knob on one end, which cytologists call a satellite. A large *S* is printed before the one that lacks the satellite. This is to represent the gene for singleness, which it carries. Its mate (homologue) has a small *s* to represent the gene for doubleness, which is recessive. The chromosomes of the eggs and pollen grains produced by this single-flowered plant are also shown. They are of two types, I and II, and half the eggs are of one and half of the other type. This is also true of the pollen grains. According to Philp and Huskins, however, only those pollen grains with the satellited chromosome function, and all the eggs live except about 6 to 8 percent of those lacking a satellite. Since only one type of pollen grain lives, there will result just two types of plants. They are shown at the lower part of the diagram.

[6] This work has recently been questioned by Vestergaard and may need further investigation.
[7] This actually happens occasionally, as discussed earlier, when a diploid sex cell is formed.

One will be single, since it receives the knobless chromosome with the single gene, and the other will be double, receiving two double-flowering (*s*) genes and two satellited chromosomes. Since there are not quite so many eggs carrying the large *S* for single flowers, the result is about 54 to 56 percent of doubles and 44 to 46 percent of singles. Philp and Huskins report that all doubles examined by them had two

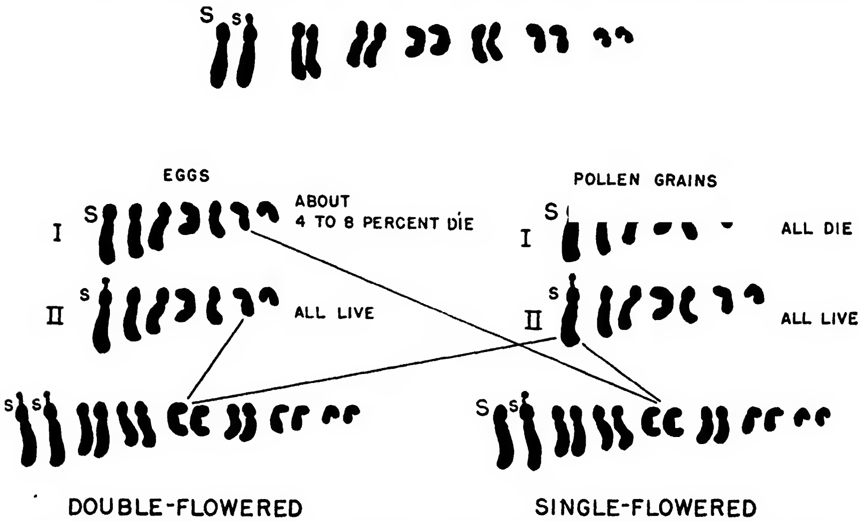

Figure 15.—The chromosome situation in ever-sporting, double-flowering stocks.

satellites, while all singles had but one. This refers, of course, only to the ever-sporting races.

Another cytologist, Frost (*135*), working with stocks, has also demonstrated the value of cytology to flower breeding. He has shown that the proportion of double-flowered plants may be increased very materially. Among the various types of stocks he had in his experimental plot was an ever-sporting form known as Snowflake. In this variety he found a peculiar single-flowered plant that had very narrow slender leaves. When this plant was self-pollinated it gave about 47 percent of singles and 53 percent of doubles. About 37 in every 100 plants had the narrow slender leaves of the parent. Also, these plants were very weak in growth and had no decorative value. The remaining normal plants descended from this narrow-leaved parent were found to be about 90 percent of doubles. Since the slender leaves are conspicuous even in the seedling stage, the plants having them may be discarded at that stage, and among the remaining plants there will be only about 10 percent of singles. In order to continue this situation, however, it is necessary that seed be saved only from the slender-leaved types.

The explanation for this interesting condition was worked out by making a cytological study of the chromosomes of the slender plants. In addition to the 14 chromosomes expected, these plants showed a small chromosome piece, which cytologists commonly call a fragment. These plants, then, had 14 + 1 chromosomes. Evidently this frag-

ment was the part that carried the gene for singleness or doubleness. Since only slender-type plants had this fragment, it was concluded that the slender leaves were also caused by its presence. Since a gene for singleness was also in the fragment, these two characters, singleness and slender leaf, behaved as linked genes do; that is, they tended to remain together from generation to generation. Thus if the slender plants are discarded in the seedling stage, it means the removal of most of the singles. This very unique scheme is not in practice as yet, probably because it is not understood by the average flower breeder.

Since the chromosome number of a plant does have considerable importance in breeding work, a list of chromosome numbers of some of the most common flowers is given in table 1.

TABLE 1.—*Chromosome numbers in some of the commoner flowers*

Name of flower	Chromosomes in— Sex cells	Chromosomes in— Body cells	Name of flower	Chromosomes in— Sex cells	Chromosomes in— Body cells
	Number	*Number*		*Number*	*Number*
Ageratum	10	20	*Dahlia variabilis*	32	64
Alyssum	8	16	English daisy	9	18
Annual larkspur	8	16	Fuchsia	11	22
Bachelor button (cornflower)	12	24	Lily, Easter	12	24
Calendula	14	28	Lily, tiger	-------	36
California-poppy	6	12	Nasturtium	14	28
Canterbury-bells	8	16	Rhododendron species	13	26
Canterbury-bells (tetraploid)	16	32	Roses, various types	7, 14, 21	14, 28, 42
China-aster	9	18	Snapdragon	8	16
Chrysanthemum	9	18	Stocks	7	14
Clematis	8	16	Sweet peas	7	14
Columbine	7	14	Sweet-william	15	30
Cockscomb	18	36	Wallflower	7	14
Dahlia (some types)	16	32	Zinnia	12	24

SOME PAST ACHIEVEMENTS AND FUTURE POSSIBILITIES

THE fundamental principles of breeding are now fairly well established, but the methods of application vary with different plants. The plant breeder who is interested in flowers and ornamental plants is faced with the problem of choosing his material from among many hundreds of species. It is obviously impossible to work with more than a small proportion of them. As a rule those breeders who have accomplished the most have limited themselves to a very few.

In preparing this article, the authors also were confronted with the task of choosing only a few representative species out of many available. In doing this it was realized that much interesting and valuable work would necessarily be left out. To some extent this omission is compensated for by the extensive appendix on research in flower breeding at the end of this article. Those especially interested in some flower not mentioned may find it included there.

AMARYLLIS

Botanically the name amaryllis should refer to the entire family Amaryllidaceae, but horticulturally it is used for plants of a single genus, *Hippeastrum*, belonging to this family.

A watchmaker named Johnson, of Lancashire, England, is credited with having produced in 1799 the first hybrid amaryllis recorded in the history of this plant. Johnson had a small garden where he followed his hobby of hybridizing plants and produced *Hippeastrum johnsoni* Bury, which even by modern horticultural standards was a distinct and outstanding variety. This hybrid is recorded as a cross between *H. reginae* Herb. and *H. vittatum* Herb. It has since been used a great deal as a parent in the production of other hybrid amaryllis.

It was at the end of the eighteenth century that widespread interest began to be centered on plants of the amaryllis family. In 1821 William Herbert published a treatise on plants included in the amaryllis family. This was followed in 1837 by his work entitled "Amaryllidaceae", which is still considered a valuable record of the amaryllis family. In this book Herbert lists under the genus *Hippeastrum* 31 "hybrid or mixed crosses" which he had secured or which had been produced by others and brought to his attention.

The family of De Graaff, of Leiden, Netherlands, was also greatly interested in the amaryllis at the beginning of the nineteenth century and produced hybrids that were of importance at that time. Following closely was the famous English firm of James Veitch & Sons, which introduced two handsome species from the Andes of Peru, *Hippeastrum pardinum* Dombr. and *H. leopoldi* Dombr., which were first flowered at Chelsea, England, in 1867 and 1869, respectively. From these two species have come many beautiful hybrids. A list of those who have made noteworthy contributions to the development of the amaryllis in the last 50 years includes such names as Arthington Worsley in England, E. H. Krelage in the Netherlands, E. L. Holmberg of Argentina, and Henry Nehrling and Theodore L. Mead of the United States.

As is the case with many horticultural plants, botanists find it difficult to classify the species and varieties of amaryllis. Because of the way plant improvement has developed in ornamental horticulture and the lack of records, it is impossible to trace the ancestry of the heterogeneous and hybrid varieties of today.

A. Worsley, writing in the Gardeners' Chronicle in 1901, stated that in his opinion a botanical classification of all the modern amaryllis varieties would divide them into but two species. *Hippeastrum vittatum* remains fundamentally as it existed 100 years ago, allowing for the superiority it has attained through selection and good culture. The other species is more difficult to trace because so many of the original characters have been lost in breeding. The type as it is now known has a short, well-expanded, large, substantial flower with wide segments and the hairy throat of *H. equestre major* Herb., the color of *H. equestre* Herb. and *H. rutilum* Herb. (rarely of *H. aulicum* Herb.), and the keel markings of *H. reginae*. The colors are now very varied. The rarer colors, especially the coppery reds and those nearest white, have of late been diligently sought and selected, and hence have increased in collections, at the expense of other colors.

It is Worsley's belief that the frequent self-colors that appear in lots of seedlings are reversions to some ancestral type, and that the first parents of all our parti-colored or marked flowers were selfs, and inconspicuously colored at that.

The confusion in the genealogy of the amaryllis goes so far as to shadow the parentage of the first recorded hybrid made by Johnson. This variety is recorded in Mrs. Bury's work published in 1831 as the progeny of *Hippeastrum formosissima* × *vittatum*. According to J. G. Baker's Handbook of the Amaryllideae, published in 1888, however, *H. johnsoni* was raised cut of *H. reginae* × *vittatum*. To Worsley both these suppositions seem untenable, for he has never been able to hybridize *H. vittatum*, and further he states that *H. johnsoni* does not bear any resemblance to *H. vittatum*. Further to complicate this matter there appear to be two distinctly different plants in the literature, both under the name *H. johnsoni*. Thus down through the list of hybrids there are many discrepancies, resulting in confusion in any attempts to trace the parentage of modern amaryllis varieties. Published descriptions frequently giving incomplete information have sometimes served further to obscure the genealogy of amaryllis.

Also to be considered is the question of sterility in hybrids. In the past doubtless many excellent but sterile hybrid amaryllis have been lost because of an incomplete knowledge of means of vegetative propagation. Fortunately the work of Ida Luyten in the Netherlands in 1926 has clarified many problems in connection with the multiplication of bulbs by asexual means.

Worsley, who is known as the dean of the amaryllis fraternity, stated in 1901 that although his efforts had been directed for many years to producing *Hippeastrum* species hybrids, he could not claim to have met with success in a single instance. He said that he was aware of but three or four undoubted species hybrids—*H. solandriflorum* × *johnsoni*; *H. johnsoni* × *solandriflorum*; *H. pardinum* × *reticulatum*; and possibly *H. reticulatum* × *vittatum*. These must be reduced to two or three if *H. johnsoni* is itself regarded as a species hybrid. He acknowledged that other species hybrids have probably been raised and the parentage left in doubt, for such species as *H. equestre*, *H. aulicum*, and the *rutilium-reginae* group are all good seed bearers when self-pollinated or when crossed with certain hybrid forms. The fact that such hybrids already have the blood of these species, he believed, accounts for the ease with which they cross back with their purebred relations.

Despite the uncertainty enshrouding the lineage of many of the varieties of modern amaryllis, breeding and selection have gone on apace, and each year more interest is being manifested in the development of this flower. In 1934 the American Amaryllis Society was launched. In its constitution its aims are stated as "the promotion of sub-order I Amarylleae, and sub-order II Alstroemerieae, order Amaryllideae." As part of its activities this organization publishes a yearbook, in which is attempted a complete inventory of all Amarylleae as well as the collecting of information from all over the world on the breeding and culture of these plants. It will contain systematic descriptions of new varieties, which will be of tremendous importance both historically and as an aid in breeding work in the future.

The American Amaryllis Society is also sponsoring national amaryllis shows, the first of which was held at Orlando, Fla., in April 1934, with 10,000 blooms. The varieties that attracted most attention were

those having blossoms of pure white or a refined shade of red. The display of amaryllis bearing yellow blossoms was not of good quality, and more breeding and selection are necessary before a pure yellow blossom can be secured.

In 1935 the second national amaryllis show was held at Montebello, Calif. The hybrid types of amaryllis exhibited by commercial plant breeders in California were the outstanding feature of this exhibition. Apparently, striking, clear colors and large sized blossoms were the characters that appealed most to the spectators at this show.

The national amaryllis show was held again in Orlando in 1936. The varieties of amaryllis of Dutch origin were the outstanding display of the exhibition. Perfection of form and color were the outstanding qualities of these varieties.

In the Bureau of Plant Industry, breeding and selection work with amaryllis have been conducted since 1909. The aims in this work have been to improve existing types of amaryllis and to obtain new colors, more shades, and a further increase in the size of the flowers, and in numbers of flowers in clusters. In 1909, 12 varieties of amaryllis were imported— Diana, Venus, Serapis, Progress, Achilles, Crimson King, Vesta, Virgin Queen, Monarch, Bacchus, Adonis, and Scarlet King. The colors ranged from dark red through pink to white with red stripes.

The late E. M. Byrnes, formerly superintendent of the Department greenhouses, undertook by cross-pollination to develop new colors from the original flowers. In 2 years' time the plants resulting from the crosses came into flower. Each year since 1909 this process of selection and cross-pollination has gone on in order to produce superior varieties.

One of the outstanding varieties of amaryllis developed at the Department greenhouses is a pure white one. This was first exhibited in 1920. Since that time this variety has been further improved in size, form, and purity of color.

Each year an amaryllis exhibition is held at the Department greenhouses. Most interest at these shows seems to be directed to the pure white flowers and those of clear, new colors. The larger flowers likewise attract much attention.

The literature fails to reveal any great amount of work on the breeding of amaryllis on the basis of our present knowledge of genetics and cytology. The fact that we have a number of supposed cases of generic hybrids in the Amaryllidaceae has created considerable interest, but it remains to be decided in some of these cases whether the botanical classification of genera has been sufficiently rigid and whether such hybrids actually are the result of crossing two distinct genera.

It is certain that cytogenetic study will be the means of elevating the breeding of amaryllis to a higher plane and of broadening its scope. One of the first steps in such a plan is to acquire and make chromosome studies of as many species as can be secured. As a result of these studies much can be learned concerning the probable parentage of some of our modern varieties. Again, cytological and anatomical studies may solve problems of apparent sterility between certain species. Chromosome studies will be of considerable help in fundamental taxonomic studies of the entire family Amaryllidaceae.

Because the amaryllis varieties are extremely heterozygous, or hybrid, in their genetic make-up, and because they can be propagated by vegetative means, it is questionable whether it is worth while to breed pure-line material that is homozygous. The time element must be considered, for with the amaryllis it takes 2 years from seed to flower while in some of the other genera of the Amaryllidaceae the time is much longer.

For the next decade it is probable that most new varieties will be derived from the hybrid kinds that now exist. However, considerably more thought and effort will doubtless be directed to careful and systematic breeding as the tools and methods of modern plant breeding become better known.

China-Aster

In popularity the China-aster (*Callistephus chinensis* (L.) Nees) is not exceeded by any other cut-flower annual with the possible exception of the earlier blooming sweet pea. The size, boldness, and attractive form of the blooms, and the sturdy stems and free-flowering habit, as well as the diversity of types available, contribute to its popularity.

A single species, native to China, is included in the genus *Callistephus*, yet this has given rise to a range of forms equaled by few of the garden flowers of today. The family Compositae includes this genus as well as *Aster*, the latter with a great diversity of species, and distinct from China-asters.

A Jesuit missionary, R. P. d'Incarville, introduced the China-aster into Europe in 1731. The original form was single, with two to four rows of ray florets of red, blue, violet, or white, and numerous yellow disk florets. The original stature was medium tall, some 18 to 24 inches in height. The "single chinensis" type now offered by seedsmen and thought to be the old original aster is a midseason type, flowering toward the end of August. Early improvement work was concentrated in France and yielded double forms such as the peony-flowered type. During the first half of the nineteenth century German breeders were so active, chiefly with quilled types, that *Callistephus* became known in America as the German aster. Double forms reached England by 1752, and a variegated blue and white type was known in 1807. By 1851 the quilled type, perfected in Germany, was well known, and dwarf types were appearing. The Comet type, dwarf and compact with lone flat rays and a loose flower head, was introduced about 1886. The Queen of the Market type, notably early flowering with wide-spreading habit and long stems adapted to cutting, appeared in the trade about 1886 from France, where it was already well known in the Paris markets. The Semple strain, tall and strong, with stiff stems and large flower heads, was developed in Pennsylvania. Other tall branching types, emphasizing strong flower stems and large size of bloom, have been developed in the United States for the florists' cut-flower requirements. Recent improvement has been accomplished chiefly by seedsmen, although the Wisconsin Agricultural Experiment Station has taken a leading part in the development of strains resistant to the fusarium wilt disease.

It is generally admitted that a satisfactory classification of China-asters, including all the forms offered by seedsmen today, is imprac-

ticable. Bailey in 1895 offered a tentative classification based on form of bloom and of florets. Beal has offered a more inclusive classification, using four classes of plant habit (tall pyramidal, tall branching, dwarf, single) with further subdivisions based on form of flower heads and florets. Seedsmen also employ the purpose of the variety in making classifications, as florists' cut-flower types, with stiff stems. One American seedsman offers nearly 200 varieties of China-asters and a European firm offers over 500.

During the last decade increasing prevalence of two diseases, wilt and yellows, threatened to wipe out the China-aster. Losses became so heavy that florists and home gardeners alike were turning to other flowers for summer and early-fall cutting, and seed sales dropped alarmingly. Partial control of both diseases has been effected as the result of recent research, in which the Wisconsin station has assumed a leading role. The wilt disease, which is caused by a soil- and seed-borne fungus of the genus *Fusarium*, has been conquered by selection of strains resistant to infection. Yellows, a virus disease spread by a species of leafhopper, may be avoided by growing plants under special cloth shelters, which exclude the insect carrier.

Jones and Riker (*274*) began selection of wilt-resistant asters in 1925. Commercial varieties were grown in "aster-sick" soil, thoroughly contaminated with *Fusarium* as a result of repeated aster culture. No one of the commercial varieties proved to be uniformly resistant to wilt, but resistant individuals appeared among most of the types tested. Selection was continued in the progeny of resistant plants through 1930. Beginning with 1929, extensive testing and selection were carried out at the Bodger Seed Co. farms at El Monte, Calif. Earlier efforts were concentrated on several flower colors in the American Branching group and on the Heart of France variety, but later study has shown that resistant lines are available within other desirable types of asters such as the Semple, American Beauty, Comet, and Royal types. Seedsmen now advertise resistant asters of all major groups except the pompons. Commercial resistant strains, maintained by selection each year, are rarely 100-percent resistant, but represent a marked advance over the unselected varieties.

In the reports on development and improvement of China-asters no mention of artificial hybridization has been found. Furthermore, the genetics of *Callistephus* seems to have been wholly ignored except for one record of an apparent mutant defect in the ray florets of a single form. All the characteristics we have in *Callistephus* today—diverse plant form and stature, divergent form and color of bloom, varying dates of maturity, resistance and susceptibility to wilt—have evidently arisen from the old original type of the species by spontaneous mutation and chance hybridization. All that man has done to improve the aster consists in growing it in immense numbers and in saving those segregates and mutants that have appealed to him as desirable.

The complete range of color now available was obtained years ago. Improvement since the early days has taken place chiefly in form of flower (fig. 16) and in plant habit. The ordinary procedure consists in saving seeds of natural variants, usually produced without protection against crossing with neighboring varieties. After a few years of

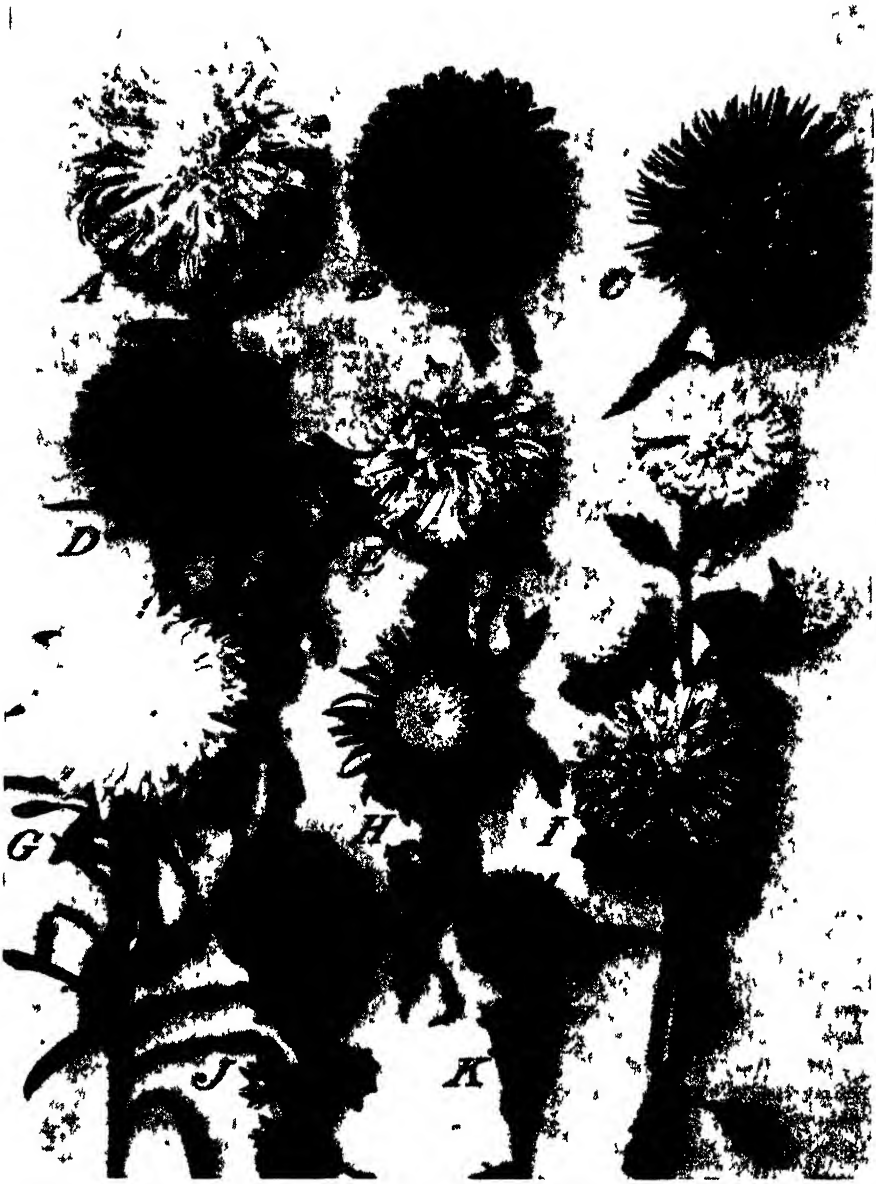

Figure 16.—A few of the many forms of asters now available *A*, Mammoth or Giant of California; *B*, Early or Late Beauty; *C*, Unicorn or Ray; *D*, King; *E*, Ostrich Plume; *F*, Queen of the Market; *G*, American Branching; *H*, Sunshine; *I*, Hohenzollern, *J*, Victoria, *K*, Tres Naive.

selection the type becomes fixed for the new character, with color variants still appearing within it. Colors are in turn fixed by further selection. As an example, the Comet type appeared on the market in

1886 as a pale pink fading to white. Six years later, rose, blue, and pure white Comet types were offered. It is commonly assumed that the percentage of natural crossing in asters is low, but Fleming (*131*) estimated that approximately 10 percent of natural crossing occurred at Summerland, British Columbia. In the earlier Wisconsin work on wilt resistance, individual plant selection was practiced under cages to exclude leafhoppers, which also insured a high degree of self-pollination.

Fleming grew the progeny of rogues in rows adjacent to the commercial strains from which the rogues were derived. From the variation shown by these open-pollinated rogue types in the next generation he presents certain tentative conclusions with respect to color dominance: white is recessive to all or to most colors; purple is dominant to red, and red to white; deep pink is dominant to white.

In future breeding of the China-aster the most important single characteristic to be sought is resistance to yellows. The search for a yellows-resistant type is complicated by the fact that affected plants develop no viable seed; hence a partially resistant type cannot be continued as a line selection. White (*544*) has noted that the Queen of the Market type, although susceptible, appears to be less severely injured by the disease than later sorts. Development of homozygous, or pure, lines by self-pollination will aid materially in segregating desirable qualities and will permit genetic analysis of such characters as color and habit.

Canna

When cannas were first recognized as suitable for ornamental purposes, they were tall leafy plants with comparatively small flowers and considerable space between nodes. A chronological history shows that *Canna indica* L. was introduced into England by Gerard in 1596. In 1762 Linnaeus listed but three species. Roscoe in 1828 admitted 21 species. Between 1830 and 1850 the younger Bouché, in Berlin, estimated the number of species at 82. Between 1840 and 1865 Année in France developed a race of garden types from *C. nepalensis* Wall. with pollen probably from *C. glauca* L. This hybrid was called *C. annaei* Andre. Dwarfer cannas with larger flowers appeared when a cross was made by Année in 1863 of *C. iridiflora* Ruiz and Pav. with *C. warscewiczi* Dietr.

From this point on, the interest in securing newer and better types increased rapidly, and there were many horticultural forms developed. As tastes for bedding cannas changed, the new varieties entering into commerce were dwarfer and the flowers larger and of higher quality. Because such types had been originally developed as a result of the work of plantsmen in France, the dwarf kinds are known as French, or Crozy, cannas. The latter name is used because many of the superior types were sent out by Crozy and Sisley of Lyons. Vilmorin of Antibes, Lemoine of Nancy, and Maron of Saint-Germain-les-Corbeil have all contributed to the garden canna as we know it today.

More recent than French cannas are the Italian or so-called orchid-flowered types. The latter name is employed because the flowers of these new cannas resemble the flower of an expanded *Cattleya* orchid. These varieties were first developed in Italy by M. Dammann & Co., at San Giovanni a'Teduccio, Naples. The Italian varieties are recorded as crosses of *Canna flaccida* Salisb., a native of the southern

United States, with garden forms and with *C. iridiflora*. They show improvement in the flowers, which have soft flowing margins and superior colors of golden vermilion.

During the latter part of the nineteenth century new canna varieties were being brought into the United States in large numbers. In 1893 Wintzer (*555*), of West Grove, Pa., became interested in the development of new varieties, with the object of improving the strain and developing new and desirable varieties suitable for "our trying climate."

Wintzer was particularly interested in producing a canna with a clear yellow bloom. As a result of continued hybridization and selection he developed the variety Buttercup. It was rather dwarf, early, and a free bloomer, held its flowers well above the foliage, dropped the faded ones, and the blossoms endured the sun without bleaching. Another quality that Wintzer attempted to develop in cannas was the production of rootstocks that would store well during long winters. He developed two pink-flowered varieties, Martha Washington and Betsy Ross, with small, hard rootstocks, a type resistant to decay in storage. Some of Wintzer's best varieties, including the white Mont Blanc, have resulted from using seedlings that were of no merit commercially but carried characters that he wished to introduce into the progeny. It is possible that in another decade the breeding of new canna varieties will be again stimulated and advanced by new practices and techniques.

The varieties of ornamental cannas offered in the trade today represent types that show great improvement over the original botanical species. There was a time about the beginning of the twentieth century when cannas were much in demand for the extensive bedding work that was then the mode in public parks, cemeteries, and other landscaped areas. In an effort to produce new forms and colors, gardeners year after year hybridized plants with desirable characteristics. In the last 20 years the popularity of bedding plants has waned, and consequently, many of the canna varieties have been lost. This makes a reconstruction of the lineage of the remaining varieties more difficult because many of the intermediate types between the true species and the modern complex hybrids have disappeared.

Even earlier, as a result of the mixing of species due to hybridization, there was considerable confusion in regard to the classification of canna varieties and the parentage of the varieties then in the trade. J. G. Baker, in England, writing in the Gardeners' Chronicle in 1893, concluded from a study of the canna literature from every available source, that the least conservative estimate could not give the genus *Canna* more than 16 species, although 90 had been listed previously. Granting that this confusion existed nearly a half century ago, activities of the last 50 years have done little more with canna classification than to aggravate the situation.

In recent years the canna has received attention in the technical field of cytogenetics. Honing (*213*) in the Netherlands, Belling (*46*) in the United States, and Tokugawa and Kuwada (*513*) in Japan have made contributions to the studies of inheritance in the canna. The work of these men contributes knowledge of practical nature, which can be adapted to the development of superior varieties of cannas for ornamental purposes. These studies have pointed out the advantages and shortcomings of triploid varieties in the canna, a type

which is desirable as an ornamental but usually not suitable for further breeding work. More details of the nature of triploid plants can be found in the paragraphs devoted to genetics earlier in this article.

Belling (*45*) in 1921 studied the behavior of homologous chromosomes in a triploid canna. This variety he secured under the name Gladiator. To the horticulturist it was a noteworthy variety, for it was sterile and the flowers, instead of setting seeds, dropped after they had matured and gave way to new blossoms. The production of seeds in ordinary fertile, diploid cannas is a detriment to continued flowering.

In nearly all cases triploid varieties are partially or totally sterile and thus often incapable of hybridization. In the past much time and labor have been expended in fruitless attempts to cross ornamental plants where one or both of the desired parents used were sterile and incapable of contributing to the production of hybrids. The work of Belling on cannas points out limitations and also opportunities in future breeding work with this plant.

Fortunately for the horticulturist, the canna is readily propagated vegetatively; consequently plants with sterile flowers, if worthy of perpetuation, can be increased in this way. Belling did find, however, that most of the 46 clones of cannas that he investigated had the diploid number of chromosomes, which is nine pairs in somatic cells. It would be from varieties of cannas with the normal nine pairs of chromosomes that high interfertility could be expected in connection with the development of new varieties.

Honing, working in the Netherlands, has published a series of papers since 1914, all concerned with technical genetical studies of the canna. He has reported on the inheritance of pigment in stems, leaves, and fruit papillae of *Canna indica*. As a result of crossing *C. indica* with *C. glauca* he obtained a single hybrid plant that in subsequent generations gave progeny that differed widely among different sowings for the factors of red leaf margins, wax layers on the leaves, and the number and color of staminodes. He also made a genic analysis of the inheritance of flower and leaf characters in the cross mentioned above.

At the Tokugawa Biological Institute, Tokyo, Japan, cytological studies were made on some garden varieties of cannas by Yoshichika Tokugawa and Yoshinari Kuwada. A report of their work was published in the Japanese Journal of Botany in 1924. It included a study of the chromosome number of various varieties of garden cannas. They found that there were either 18 (diploid) or 27 (triploid) chromosomes in the varieties coming under their observation.

These cytological studies in Japan also pointed out that the process of meiosis in canna is generally of somewhat abnormal tendency both in the diploid and triploid varieties. This abnormality of division is possibly the cause of some sterility, which is well recognized in certain canna varieties. Finally the work of Tokugawa and Kuwada showed conclusively that the triploid cannas are larger than the diploids with respect to the stomata openings of the leaves, the size of the cells of the epidermis of the staminodia, the thickness of the leaves, and lastly, the size of the entire flowers. It was also noted that the staminodia of the triploid plants not only are larger than those of the diploid plants but also present a desirable delicate wavy appearance

in their surface. While this Japanese paper is a technical treatise, it serves as a valuable addition to the knowledge that a practical breeder of cannas must have to carry on his work effectively.

Carnation

The carnation (*Dianthus caryophyllus* L.) is one of the oldest flowers still under cultivation. It was first mentioned and described in 300 B. C. by a Greek philosopher, Theophrastus. The original type was a single flower with five petals, measuring about 1 inch in diameter and of a pinkish-mauve color. It grew wild over much of Europe, and it still existed in Normandy as late as 1874.

In England, during the reign of Queen Elizabeth, William Turner published an extensive description of this flower. By this time the double form had made its appearance and already existed in a wide range of colors. Just when or how the double form arose will probably remain an unsolved mystery. The flower was very popular in England, and early in the eighteenth century it was used in a successful cross with sweet-william. Most of the early selection work was done by English amateurs, who rapidly developed a wide range of forms and colors. They were interested both in the outdoor garden types and in the large, double-flowered varieties of the florists. In this article the discussion deals almost entirely with the latter type, which is now one of the most important flowers grown under glass in this country.

The florists' carnation occurs in three distinct forms, the single, the double, and the superdouble, or bullhead. The second type includes all the commercial varieties. The bullheads are so extremely double that the calyx splits badly as the flower expands. The first published report that threw some light on the question of inheritance of doubleness appeared as an abstract in the 1904 Proceedings of the American Society for Horticultural Science. At that time Norton (*396*), of the Department of Agriculture, told of some experiments he was carrying on in the breeding of carnations. He reported that from the seed of individual capsules he secured all three types of carnation flowers. From one there were 6 doubles (bullheads), 15 semidoubles (commercials), and 7 singles; from another 74 doubles, 147 semidoubles, and 52 singles. These proportions are approximately 1 to 2 to 1, and they agree fully with what is expected in the progeny from a hybrid when one of the two genes affecting the same character is not fully dominant to the other. At that time Norton suggested that the practical florist should cross the single with the extreme double type and thus secure a greater proportion of intermediate true florists' types. The common practice, which still persists, was to cross two commercial double varieties, and always a large proportion of resulting seedlings were singles and bullheads.

In 1907, at the meeting of the American Breeders' Association, Norton (*397*) reported that several crosses between singles and extreme doubles, made in 1905–06, yielded 250 seedlings, which were, with one exception, commercial doubles. Since no protection from outside pollen was used, the one single seedling may have been an outcross. It was pointed out that single and very double seedlings were usually discarded no matter how desirable their other characters

might be. By pollinating a good single with the pollen of an extreme double that has some new desirable quality, a complete series of standard double seedlings can be secured, some of which may show the new character.

In 1912 Stuart (*498*) presented a more comprehensive publication on this question. The breeding work, begun at the Vermont Agricultural Experiment Station, was completed at the Arlington Experiment Farm, Arlington, Va., after Stuart joined the staff of the Department. The earlier work of Norton was confirmed and the following facts established: When a single was crossed with a single, all the hybrids were singles; a single crossed with a commercial double gave about 1 single to 1 commercial, but when crossed with a bullhead it gave practically all commercial doubles; when 2 commercial doubles were crossed they gave about 1 single to 3 doubles. Unfortunately the doubles in Stuart's report were not classified as to bullheads and commercial types.

The results were analyzed as follows: (1) The commercial carnation as grown by florists is an unfixed hybrid from a cross between a single and superdouble; (2) the bullhead type is incompletely dominant to the single, and the hybrid resulting from crossing them is the intermediate or so-called commercial double.

Unfortunately, the development of superior double carnations is not so simple as the preceding account seems to indicate. Frequently the investigator is hampered by having abnormal plants appear in his progenies, from which very little or no seed can be secured. According to Connors (*81*) and his associates, who carried on carnation breeding at the New Jersey Agricultural Experiment Station for 15 years, there are many types of carnations with respect to the relative development of pistils and stamens. These types include plants bearing male flowers only, plants with all stamens transformed into petals, and asexual types in which pistils and stamens are rudimentary and nonfunctional. It was possible to further subdivide these groups so that 10 types in all are recognized.

In spite of the many difficulties and the meager information on inheritance in the carnation, a very large number of choice varieties have originated as seedlings. Many florists have devoted considerable space and time to this work. One of the leaders was Ward, who devoted considerable time to the production of better florist types and presented his observations on carnation breeding (*533*). At that time he stated that in raising varieties from hybrid seed very few improvements are produced. He estimated that only about 1 in 1,000 seedlings had any merit, and probably but 1 in 5,000 or 10,000 was a decided advance. He also felt that even this low frequency would decrease rather than increase because of the higher standard that was set from year to year.

The list of seedling varieties is constantly changing as old ones are replaced by newer and better types. It has been the practice of many commercial growers to try out a small number of some of the new ones each year. It may happen that one from New England is very inferior in the Colorado section, and one from Colorado may lack quality in Illinois. This has demonstrated, in this country, that it is necessary to develop varieties for a given locality.

Many carnation varieties originate as bud sports. It is a relatively simple matter to propagate these if desirable. These sudden changes may affect any part of the plant. Sometimes the leaves are broader, or deeper or lighter green, or the plant is dwarfer, more compact, or taller. The flower may be modified as to color, size, length of stem, or structure of petals. Since the flower is of primary importance, bud sports are most likely to be noticed when floral characters are involved.

Unfortunately there is no authentic evidence on the frequency of bud sports in carnations. Isolated observations in various sections of the country seemed to indicate, however, that they might occur at a rather high rate. Unquestionably many of the best of our current varieties arose in that way. As a result growers have become accustomed to keeping a careful watch over their benches during the growing season. Since, under the stress of commercial operations, there is always the possibility of mechanical mixture of rooted cuttings, it is impossible to give an accurate account of the situation.

There are a number of carnation disease problems in the solution of which the plant breeder should be useful. Two of these diseases, carnation rust (*Uromyces caryophyllinus* (Schrank) Wint.) and stem rot (*Corticium vagum* B. and C.) may at times become very troublesome. Varieties resistant to these diseases, provided they were also of high quality, would be very acceptable. There is some evidence that resistance to rust already exists in some of the better commercial varieties. In 1932, a test of 36 varieties was made at the Waltham Field Station, in Massachusetts, and they were grouped for rust resistance as very susceptible, moderately susceptible, slightly susceptible, and resistant. The standards for grading resistance were not stated, nor were the severity and uniformity of the infection given.

The problem of color inheritance has received very little attention as yet. The highly heterozygous conditions of the carnation and the very frequent functional sterilities encountered have discouraged research along these lines. As facilities for flower breeding are increased, it is likely that some attention will be given to these problems.

The condition known as carnation splitting is another problem that should receive more attention from the flower breeder. It was studied by Connors, who stated that it was caused by two conditions—the formation of an unusually large number of petals through transformation of stamens and pistils, and the development and growth of secondary buds within the flower.

As early as 1903, Ward had assumed that splitting was entirely hereditary, and he advised the selection of seedlings that produced flowers with an unsplit calyx. Later, Connors stated that the experience of the New Jersey station indicated splitting was influenced by both hereditary and environmental factors. It is needless to say that a good nonsplitting variety would be a valuable contribution.

Since there is a rather definite regional adaptation of varieties, it seems that a sound carnation breeding program should include facilities for testing all seedlings in as many different locations as possible. When the work is carried on at only one location, there is loss from discarding seedlings that might prove very valuable in another region.

Chrysanthemum

The culture of improved forms of chrysanthemums antedates the beginning of the Christian era by several centuries. Apparently they are native to China, and are mentioned in Chinese literature as early as 500 B. C. The Japanese grew them extensively at an early period and did considerable work in developing improved types. A form with 16 petals was chosen as the flower emblem of the Emperor. In both China and Japan, single-stemmed varieties were generally grown long before the plant was introduced into western Europe.

The earliest record of chrysanthemums in Europe is of an importation in 1688. It seems strange that this attractive flower was not known to Europeans at an earlier period. The following year several varieties were reported as being grown in the Netherlands, but for some unknown reason they soon passed out of cultivation.

It was not until 1764 that chrysanthemums made their appearance in England. They soon became popular, and additional varieties were imported from China in 1789. During the following 20 years, eight new types were introduced from China.

All the early varieties introduced into Europe were brought in as living plants. The first attempts to grow seedlings were not made until about 1827. At this time a Frenchman, M. Bernet, flowered several fine seedlings from seed he found in withered flower heads the previous autumn. Following this it is very probable that many amateurs began to grow seedlings, but unfortunately we have no records of any new developments.

In 1846 Robert Fortune brought two small-flowered varieties from China and introduced them into English gardens. They were not well received by the English, but when sent to France they soon became rather popular and were used extensively in hybridizing. It seems probable they were the progenitors of our modern small-flowered varieties.

The early history of chrysanthemums in the United States is rather obscure. According to the 1828 catalog of William Prince, they were introduced into Hoboken by John Stevens in 1798. The plants were probably a dark purple form, which had reached Europe from China in 1790. In 1826 the Prince's Nursery listed 26 varieties, and by 1835, according to Hovey's American Gardener's Magazine and Register, 50 distinct varieties were available in this country.

There is no record of the origin of any of these early chrysanthemums. Propagation by cuttings was very simple, and strains were perpetuated in this way. Undoubtedly this was a strong factor in retarding breeding. The fact that so few different types existed in this country in 1835 is an indication that very little actual improvement by breeding had been attempted.

One of the earliest breeders in this country was Robert Kilvington, of Philadelphia, who exhibited a new seedling named William Penn before the Pennsylvania Horticultural Society in 1841. It was a large white double flower, almost globular in shape. It seems strange that this did not immediately stimulate more work, but no other contributions appeared for some time. About 1850 Samuel Brookes, of Chicago, became very much interested in chrysanthemums and did considerable work to stimulate interest in the flower.

A general interest in chrysanthemums was slow to develop in this country. In 1844 an impressive display was made of many of the available varieties at the fall show of the Massachusetts Horticultural Society. Two years later there was a large exhibit before the Pennsylvania Horticultural Society, where the chrysanthemum was described as the coming flower. A special chrysanthemum show was not held, however, until 1868. At present there are many chrysanthemum exhibits each year.

Previous to 1850, chrysanthemums were not grown as greenhouse plants. About this time a few varieties were tried under glass, and development of special florists' types was soon under way. The development of this branch of the florists' business soon extended the blooming period and made it possible to market the large showy types that were being introduced from Japan. About 1883, Hosea Waterer imported about 50 varieties from Japan. Shortly following this, a large white variety appeared that was so attractive it is said to have been sold for a fabulous sum. This variety was sent to Mr. and Mrs. Alpheus Hardy by an appreciative friend in Japan. It was named Mrs. Alpheus Hardy and undoubtedly was one of the stimulating influences that led to a quickening of interest in chrysanthemum breeding in this country. Some of the successful breeders of this period were T. H. Spaulding, E. Fewkes, Pitcher & Manda, V. H. Hallock, W. C. Pyfer, E. G. Hill, and F. Dorner & Son. By 1894, there were listed 163 varieties of American origin.

In the latter years of the past century, one of the most prolific of modern chrysanthemum breeders, Elmer D. Smith, of Adrian, Mich., began his work. He had introduced 445 new varieties by 1928, and many others have been added since that time. Other American breeders who contributed many new chrysanthemums during this period are E. M. and J. W. Byrnes and F. L. Mulford, of the Department of Agriculture. More recent entrants in the work have been V. R. De Petris, of Detroit, Mich., and Alex Cumming, Jr., of Bristol, Conn., who has specialized with outdoor chrysanthemums.

The efforts of these breeders have been mainly to develop greenhouse or so-called forcing chrysanthemums. A program to develop hardy outdoor types has been under way in the Department for some time. The work was started by growing outdoors as extensive a collection of varieties as possible, and securing data on their time of bloom and winter hardiness. The work was carried on at first at the Arlington Experiment Farm, but in recent years certain selections have been sent to various cooperating State experiment stations for trial. By selecting each year the earlier flowering types and growing seedlings from them, races have been developed that bloom as early as July in the vicinity of Washington, D. C. (fig. 17). The earliest strains are followed successively by others until heavy frosts kill the plants. The work has demonstrated very clearly that time of bloom is actually a hereditary trait transmitted from parents to seedlings.

The problems involved in chrysanthemum breeding are to some extent very similar to those faced by the rose breeder. The history of the early chrysanthemum varieties is not known, but it seems likely that most of them arose as mutations or bud sports from other varieties. While there are no data on this point, the evidence all points in

that direction. So far as can be determined, little or no breeding work was attempted in China or Japan, and all varieties were maintained by the rooting of cuttings. If a new color or other bud sport appeared, it was simply increased by cuttings and soon became established. Had the Japanese and Chinese been growing seedlings there would certainly have been many more varieties available in

Figure 17.—The chrysanthemum breeding plot at the United States Horticultural Station, Beltsville, Md., where hardy early-blooming varieties are being developed Already a wide range of types and colors have been developed, and the blooming date continues from late July to killing frosts. In the background are cages built over 8 plants to protect them from cross-pollination.

those countries when the flower was first brought to Europe. This point is strikingly confirmed by the fact that Smith was able to develop over 450 new seedling varieties in a little over 30 years. Some of these may have been bud sports, but by far the larger number were seedlings.

The keeping of parentage records has been fairly thoroughly done by some breeders. Since the modern chrysanthemum is really of rather recent origin, and probably does not involve a very complex mixture of species, such records should have some value. If they all were available it seems very likely they would show that certain parents produce more good seedlings than others. While there is little or no scientific data on the inheritance of plant characters in chrysanthemums, breeders have learned through experience that certain varieties are likely to transmit their flower color. The variety Harvard, for example, usually produces red seedlings in crosses, and Thanksgiving Pink transmits its pink color. These observations seem

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to indicate a probable dominance of these colors over other shades, and also that these varieties may be pure for their respective colors.

One of the greatest difficulties encountered by the chrysanthemum breeder is the failure of many fine varieties to set much seed. In some instances this may be due to an actual sterility, but it is generally the result of the extreme doubleness of the flower. Not much can be done about this unless a single can be found, which when crossed with a double gives all double seedlings. Under such conditions, all crosses could be made with the single as maternal parent.

The production of bud sports or mutations has also played a rather important role in the development of the chrysanthemum. The mutation tendency is undoubtedly higher in some varieties than in others. In the absence of any scientific data we are forced to rely on general observations as to the frequency of such changes. According to some growers, the sport of a variety very frequently reverts to the parent type. The mutations that have been observed are mostly flower color changes. Very probably there are others affecting foliage and other characters.

The possible causes underlying the sudden appearances of bud sports are mentioned in another section of this article. If more were known about them we might be able to produce controlled mutations in greater numbers. If they result from some environmental influence, then varieties of chrysanthemum must differ markedly in their response to it, because some varieties mutate more readily than others. This indicates an inherent mutation tendency. In other words, chrysanthemums may have some rather unstable characters and may mutate under certain environmental conditions.

Dahlia

Francisco Hernandez, physician to Philip II of Spain, was sent on an expedition to New Spain (Mexico) in 1570. The purpose of this journey into the New World was to study the natural history of this intriguing land to the westward. After Hernandez returned to Spain he published in 1615 four books on the plants and animals of Mexico. In one of these books he described three types of plants which nearly 200 years later were to be called dahlias. To these three plants he gave the Aztec names acocotli, cocoxochitl, and acocoxochitl, which mean; respectively, "water pipe", "hollow-stem flower", and "water-pipe flower", the allusion being to the hollow stems of the plants.

From Hernandez's writings it is apparent that the Aztecs had worked on the improvement of these plants, for this report indicates that they varied in color, form, and degree of doubleness. The illustrations he published show that somewhat double dahlia flowers existed in Mexico in the sixteenth century.

Vitalis Mascardi in 1651 published a work in Rome in which there is an illustration of a double-flowered dahlia. Again, in 1787, a Frenchman, Nicholas Joseph Thiery de Menonville, searching in North America for the valued cochineal bug, described dahlias, growing in a garden near Oaxaca, which had large asterlike flowers, stems as tall as a man, and leaves like those of an elder tree.

It was not until after 1789, however, that the Old World awakened to the possibilities of the dahlia as an ornamental plant. In this year

Vincente Cervantes, director of the Mexican Botanic Gardens, sent to the Royal Gardens in Madrid seed of dahlias from Mexico which were destined to play a tremendous part in the development of the superior types of garden dahlias as we know them today. It was to Abbe Cavanilles, director of the Royal Gardens, that these seed were sent, and from them were produced flowers of brilliant hues typical of the dahlias to be found growing in Mexico.

Cavanilles named this plant, which was practically unknown in Europe, Dahlia, after Andreas Dahl, an eminent Swedish botanist living in Berlin, who had been a pupil of the great Linnaeus. Among the plants that Cavanilles received from Mexico he recognized two species, *Dahlia pinnata* Cav. and *D. coccinea* Cav. The former, which showed great variation in its progeny, has since been called *D. variabilis* Desf. and *D. rosea* Cav., but according to the rules of botanical nomenclature the name *D. pinnata* must stand. *D. coccinea* does not cross readily with other species, and its flower color is confined to scarlet and shades of orange.

At the time Cavanilles received the shipment of dahlias from Mexico a great deal of interest was being manifested by botanists and plantsmen of Europe in plants from the New World. Within a few years seeds of the dahlia were sent to a number of botanic and private gardens in Europe. In 1798 seeds were sent to Kew Gardens in England, but apparently plants from the seeds died before they reached maturity. By 1803 an English plantsman had flowered *Dahlia coccinea*, for in Curtis' Botanical Magazine of 1804 appeared a colored figure with the statement, "Our drawing was taken in June 1803 at Mrs. Fraser's, of Sloane-Square, who has the credit of introducing this ornamental plant among us from France."

From 1804 to 1806, shortly after Alexander von Humboldt sent seed from Mexico to Paris and Berlin, a phenomenal increase in the number of dahlia varieties occurred. Within 12 years nearly every color that we have today had appeared in the flowers. In 1806 the Berlin Botanic Gardens had growing 55 single and semidouble varieties. Two years later the first perfect double dahlia was raised by Hartweg at Karlsruhe, and the year following a variety with single white flowers was developed.

By about 1810 the dahlia became exceedingly popular and growers sought assiduously to improve and create better double flowers within the genus. Both in the British Isles and on the Continent new forms, showing doubleness and brilliant colors, were developed. In the Botanical Magazine for 1817 an illustration revealed a rose-colored dahlia that originated in France and showed the form of the decorative dahlia as the type is now known.

From 1810 to 1850 interest in the dahlia increased tremendously. The ease with which hybrid seed could be secured, because of relatively self-sterile flowers, the short time required to produce new varieties, and the extreme variation secured both in sizes and colors of the flowers all contributed to the popularity of this new plant. Of particular interest in revealing the quality of dahlia varieties of that time is The Annual Dahlia Register for 1836. This contains particulars of the introduction of the dahlia into England and, most important, has as illustrations upward of 50 highly colored figures of dis-

similar dahlias. It also contains an index of 700 varieties of the dahlia that were recognized as such at that time. The illustrations in this book show double flowers exclusively, all with a colorful array of petals in very dense, round heads, arranged very geometrically. It was this stiff, formal, double flower that was so popular in the first half of the nineteenth century, and the type in which interest waned to a marked degree in Europe shortly afterward.

Seed of the modest dahlias that had been sent abroad from North America were returned to their native shores and yielded plants with flowers of an endless array of color patterns and degrees of doubleness. In the United States the craze for new dahlia varieties was nearly as acute as it was in Europe, and likewise, interest in the stiff, formal flower began to wane about 1860.

The first National Dahlia Society was organized in Great Britain in 1870, and about that time the diminutive pompon type of dahlia was developed, but these two events did not serve to recreate any great amount of interest in varieties then existing.

About 1864, however, an event happened that brought renewed interest in the dahlia through the discovery of a species with characters far different from and superior in many ways to those in the dahlia varieties known at that time. One M. J. T. Berg, of the Netherlands, received a collection of plants from Mexico. Included in this shipment was one dahlia root with just sufficient reserve food remaining within it to send up one shoot. In the fall this shoot produced a brilliant, blood-red flower of a shape never before recorded. The quilled petals, typical of the dahlia of that time, were lacking, and in their places were petals that were recurved, with pointed ends. The plant was tall and sturdy and carried its flower well above the foliage.

This new dahlia was given the name *Dahlia juarezii* Hort. in honor of the then President of Mexico. It received the name "cactus dahlia" because of its resemblance in form and color to the blossoms of a cactus. This plant was to play an important part in the development of superior varieties and to become the progenitor of two new classes of dahlias, now collectively referred to as the cactus and hybrid-cactus types. The species reached England and was first illustrated in the Gardeners' Chronicle in 1879.

All efforts to trace the origin of this new dahlia failed until 1916, when Wilson Popenoe discovered the probable ancestral home of *Dahlia juarezii* in Guatemala. The primitive species he found there has a single row of eight long, spreading, crimson rays turning backward along the margin. This species was named *D. popenovi*, and it is believed to be one of the ancestors of *D. juarezii*.

It was fortunate that *Dahlia juarezii* was discovered, for in the latter part of the nineteenth century there was, both in the United States and abroad, a reaction against formalism in all arts. The stiff formal dahlia flowers that had been the rage for the past half century were outmoded. This served as a challenge to the breeders of dahlias, and, having in their possession a new species of dahlia exhibiting characters that were in demand, they began to breed new varieties to suit the public's fancy.

This activity went on for a number of years, and the progeny resulting from crosses with the new-found *Dahlia juarezii* created

great interest, particularly at dahlia exhibitions. The very fact that the flowers were displayed mostly at flower shows, however, ultimately created still another problem for the plant breeder. Interest had been centered chiefly in new and superior blossoms, while the structure of the plant upon which these flowers were borne was neglected. Consequently the new varieties possessed very weak stems and were suitable only for cut-flower exhibition purposes. As interest in outdoor displays developed, breeders were faced with the task of increasing plant vigor to reach parity with the excellence of flower quality.

Within the last 20 years much has been accomplished in securing superior varieties of dahlias. Varieties having weak short stems have gradually been supplanted by more vigorous types, and breeding has reached a high level. The number of named varieties now existing is well over 7,000, for in 1924 J. B. S. Norton published a book entitled "Seven Thousand Dahlias in Cultivation", and the number has been added to greatly since that time.

Many dahlia societies have been organized in both the United States and Europe and these have stimulated interest in the improvement of dahlia varieties. In the United States the American Dahlia Society has functioned for two decades. One of its outstanding activities is the publication of a quarterly bulletin dealing with all aspects of the culture and breeding of the dahlia. This organization also stimulates interest in the development of superior varieties by conducting flower exhibitions and trial gardens where new varieties are grown, evaluated, and exhibited.

These developments have led to considerable confusion in attempts to classify, especially for exhibition purposes, the various garden types now existing. In an effort to simplify the classification of the host of new varieties that have been developed, the American Dahlia Society had adopted a classification based on the form and size of the flower. Fourteen classes are provided for the systematic arrangement of all the various types of dahlia flowers. A number of these classes are subdivided according to the size of the flower.

Other countries also have their classifications for dahlias. A great deal of pioneer work in this direction was performed by the Royal Horticultural Society and the National Dahlia Society in Great Britain.

Worthy of special comment in considering the development of superior dahlia varieties are the trial grounds where new varieties are grown, studied, and evaluated. The American Dahlia Society has such a garden in cooperation with the Connecticut State College at Storrs. Each year a field day is held at the trial grounds, when new varieties are inspected and evaluated. Competent judges pass on the merits of each new variety, and thus the value of new kinds can be impartially reported to those interested in dahlias. Other trial grounds are conducted by State and regional dahlia organizations; these plots permit the study of the same variety under varied climatic and other environmental factors.

Scientific research has revealed in the dahlia an interesting story of the inheritance of color. In the comparatively new field of cytogenetics, investigations conducted by Lawrence (*310, 311*), curator, the John

Innes Horticultural Institution, Merton, England, are noteworthy. This work indicates how the lineage of dahlia species and varieties can be studied by modern scientific methods. Lawrence found that the colors in all available dahlia species fall into one of two color groups: (1) Pale to deep magenta over ivory-white ground color, and (2) orange to scarlet over yellow ground color. One important exception Lawrence noted was that in the so-called species *Dahlia pinnata*, more popularly known as *D. variabilis*, which is considered the source of most of the garden varieties, the flower color is made up of a combination of both of these color groups. Furthermore, through cytological studies, he found that this same plant has 64 chromosomes in the vegetative cells, or twice the number usually found in species of the dahlia. These two facts indicated that *D. pinnata* is itself a hybrid. Such work, besides aiding the taxonomist in systematizing dahlia nomenclature, is of value to plant breeders in their efforts to produce superior varieties of plants.

Lawrence's work also dispelled the widespread erroneous belief that the extreme variation of *Dahlia pinnata* showed the degree to which a species could vary following domestication. This extreme variation was shown to result from the complex genetic make-up of a hybrid which combined various specific characters brought together during the descent of the genus *Dahlia* from a primeval stock. This coupled with multiplication of chromosome numbers probably accounts for the present variability of the stock.

The dahlia, like many other perennial ornamental plants, is readily propagated vegetatively. As a consequence it is not necessary to develop lines that are pure or homozygous, as is necessary with plants propagated from seed, in order to perpetuate the same characters in subsequent generations. Ease of vegetative propagation of the dahlia is particularly fortunate because its self-sterility enforces cross-pollination, thereby maintaining a high degree of hybridity in the genus and making pure-line breeding laborious and difficult. Despite these complications, however, the development of reasonably pure-breeding stocks may have to be undertaken in the future by plant breeders, not so much in order to produce dahlias of superior ornamental value as to develop types resistant to or immune from plant pests.

Gladiolus

The superior varieties of gladioli grown today have been developed largely through work that began scarcely more than a century ago. It may be assumed from ancient writings that the Greeks and Romans made use of native gladiolus species for ornamentation, and it is certain that there were species of the gladiolus, known as Corne Flags, in Britain as early as 1597, when they were recognized as important garden plants by Gerarde. But it was not until 226 years later that the first important hybrid gladiolus was produced.

Interest in Europe was at first limited to the species native to southern Europe, Asia, and Persia. They numbered but 15 and were never very popular with gardeners. Early in the seventeenth century the development of these species came to a standstill. It was more than a century later, when new species first started coming in from southern Africa, that renewed interest was gradually stimulated in the gladiolus.

In the eighteenth century botanists and explorers became increasingly aware of the new species of plants to be found around the Cape region of Africa, but it was not until the close of that century, when the Cape of Good Hope became subject to Great Britain, that large importations to Europe were received. William Herbert, dean of Manchester, seems to have been one of the first to recognize the value of the Cape species of gladioli, for in 1820 he wrote:

I am persuaded that the African Gladioli will become great favorites with florists, when their beauty in the open border, the facility of their culture, and the endless variety which may be produced from seed by blending the several species are fully known, nor will they be found to yield in beauty to the Tulip and Ranunculus.

Dean Herbert, besides contributing valuable information to horticultural literature, was also an enthusiastic cultivator of gladioli and was regarded as an authority on Cape bulbs. He carried on considerable hybridization with the species of gladioli and recorded in the horticultural literature a large number of his successful crosses.

During Dean Herbert's time the first important hybrid appeared at Colville's Nursery, Chelsea, England, in 1823. It was derived from *Gladiolus tristis* L. var. *concolor*, with *G. cardinalis* Curt. as the pollen parent. This new variety was given the Latin name *Gladiolus colvillei* Sweet and was known commonly as Colville's corn flag. It was described as being tall and vigorous with flowers of bright scarlet with lanceolate blotches of white on the three lower petals. There are today several named varieties persisting in the trade that came directly from this outstanding hybrid. In the United States they are generally grown under glass in the East but will grow out of doors successfully in the milder climates along the west coast.

Fifteen years later the second important hybrid, which was named *Gladiolus ramosus* Paxt., was produced in France. It was first flowered by M. Rifkogel in 1838. Records indicate that this hybrid resulted from a cross between hybrids of *G. cardinalis* and *G. oppositiflorus* Herb. It bore a tall flower spike with heavy broad leaves. The flower was openly funnel-shaped and bright red with deep blotches at the bases of the three lower segments. The fact that it bloomed later than other varieties of its time made it important for at least the next 20 years.

Until 1841 there was a mild yet increasing interest in gladioli, particularly among amateurs, but that year a variety was introduced that caused the greatest stimulation ever evidenced in the history of gladiolus breeding. M. Beddinghaus, gardener to the Duke of Aremberg, had been breeding gladioli for a number of years, securing for this work as many species as were then available. Louis van Houtte, of Ghent, Belgium, realizing the potentialities of one of M. Beddinghaus' productions, immediately purchased the stock, and in 1841 *Gladiolus gandavensis* Van Houtte was introduced to the world. Van Houtte named this gladiolus after the city of Ghent and described it in glowing terms as bearing majestic flowers, numbering 18 to 20, of the most charming vermilion, the inferior petals adorned with chrome, amaranth, and brown. For a long time there was considerable controversy concerning the parentage of *G. gandavensis*. It is now accepted that this new variety resulted from a cross between *G. psittacinus* Hook.

and *G. oppositiflorus* or between hybrids from these species. Napoleon III heard of this variety, which had "created a furor in the gladiolus world", and some of the plants came into the possession of Souchet, gardener to the Emperor at the court of Fontainebleau. Souchet, using *G. gandavensis* as one of the parents, developed many new hybrids, which in time were the talk of Europe.

In England Dean Herbert kept in close touch with new gladiolus varieties and continued the pioneer work he had started, using new species and varieties in his breeding work as they became available. Representing the trade in England, James Kelway, the founder of the Langport firm, was alert to the rapid development of the gladiolus and secured hybrids from Souchet in France to develop them further and make them available for sale in England.

Queen Victoria's visit to Fontainebleau in 1855 is reputed to have stimulated a tremendous interest in the gladiolus, for she saw and greatly admired the new varieties developed by Souchet and exhibited by Napoleon III. By 1880 over 2,000 named varieties had been developed that showed characters derived from *Gladiolus gandavensis*.

Victor Lemoine was greatly interested in the development of new gladiolus varieties and the next race of hybrids of considerable importance resulted from his work at Nancy, France, around 1880. Crossing *Gladiolus gandavensis* with *G. purpureo-auratus* Hook., which was introduced in 1872, he obtained a race called *G. lemoinei* Hort. These varieties were characterized by their large flowers and the prominent blotches in the throat of the florets.

Meanwhile Max Leichtlin, of Baden-Baden, Germany, crossed *Gladiolus gandavensis* with *G. saundersii* Hook. f., which had been introduced from the Cape in 1870, and *G. leichtlinii* Baker was produced. This stock was ultimately purchased and imported by John Lewis Childs, of Long Island, N. Y., and renamed *G. childsii*. W. Van Fleet crossed a variety of *G. childsii* with *G. cruentus* Moore and secured, among many others, his famous variety Princeps. The *purpureo-auratus-gandavensis* hybrids developed by Lemoine were crossed by him with *G. saundersii* and a new race called *G. nanceianus* Hort. resulted, which was characterized by plants having remarkably large, open flowers with contrasting color mottlings in the throats.

Gladiolus primulinus Baker has been the most recent introduction to greatly influence the development of gladiolus varieties. This species was found in the Rain Forest near Victoria Falls on the Zambezi River in Africa. It was successfully introduced and flowered at Kew Gardens, England, in 1890. Since then it has played an important role in modifying gladiolus flower form and color. French, English, and American plant breeders have all taken part in developing new varieties with some of the characters of *G. primulinus*. The most outstanding characters it transmits are a light and graceful flower stem, a more or less pronounced hooding of the flowers, and a subduing of brilliant hues to soft pleasing colors. In turn the progeny from *G. primulinus* have been improved by increased flower size and more vigor in the flower stem.

Noteworthy also are the ruffled gladioli, which have been developed in the United States by A. E. Kunderd, at Goshen, Ind., starting about 1907. Later he also developed a strain having fringed and laciniated

segments, which has created much interest. Foremost among the Canadian pioneers in the development of the gladiolus was the late H. H. Groff, of Simcoe, Ontario. About the end of the nineteenth century he had developed a strain called Groff's hybrids, which were considered noteworthy, particularly because of the wide range of color they possessed.

At the present time there are many amateurs and professional and commercial growers deeply interested in the breeding of new and superior varieties of gladioli in the United States. The American Gladiolus Society, organized in 1910, did a great deal to encourage the production of new and finer varieties, as well as to straighten out nomenclature. It publishes a monthly, the Gladiolus Review, in which registrations of new gladiolus varieties are included. This organization sponsors affiliated State and regional societies and conducts an annual gladiolus show where new varieties are exhibited and evaluated.

Governmental agencies have also contributed to the development of the gladiolus. Particularly noteworthy is a series of publications during the last 20 years from the New York State College of Agriculture, Cornell University, by A. C. Beal, A. C. Hottes, and A. M. S. Pridham of that institution on the development of superior varieties of gladioli. At Cornell University there is a test garden in which most of the available species and varieties of gladiolus have been grown and studied. Likewise, at the New York Botanical Gardens a collection of gladiolus species is maintained.

Recently a technical paper has appeared written by Bamford (*10*), of the Maryland Agricultural Experiment Station, who collected many gladiolus species and varieties and made detailed chromosome counts. His work greatly expands similar studies on the same subject by M. Ernst-Schwarzenbach (1931) in France and by McLean (*326*) in the United States. Such cytological studies are of great help to the geneticist in his attempts to classify material and breed superior varieties.

This brief discussion serves to direct attention to the great complexity of the inheritance of modern gladiolus varieties. Original species have been combined and hybrids have been crossed and recrossed until the resulting multiple hybrids possess characters derived from many different species. Superior characters have been combined and varieties have been selected covering a wide range of usefulness, from the requirements of the florist who forces plants under greenhouse conditions to those of the amateur flower lover who demands a wide range of color and form for flowering through the summer.

How much more can be accomplished in the development of the gladiolus is a matter of speculation. When it is realized, however, that less than a score of the more than 150 known species have been used to any extent in the development of over 2,500 varieties of gladiolus in commerce at the present time, it seems probable that present and future plant breeders can still draw from the remaining species to give to the world even more desirable gladioli than we now enjoy.

Hemerocallis (Daylily)

The daylilies had not received much attention from breeders until the last decade of the past century. Previous to this a few species had been grown in Europe. They were first mentioned by Pena and

Lobel in 1570, when these authors described what is probably the common Lemon daylily. A few years later Lobel described a second species with single cinnabar-red flowers. These two were apparently the only ones known in Europe for the next 200 years. Unfortunately little is known of the situation in China and Japan before the nineteenth century.

In 1768 a third type was mentioned in Europe, but its exact origin is unknown. It was regarded by some as being a minor variety of one of the two older established types. About 1798 another new type appeared, this time imported from the Orient into England. No new ones were introduced until about 1934, when a semidwarf form was brought in from Japan. In 1856 another semidwarf appeared, and this was followed in 1860 to 1864 by double-flowered forms.

The first actual breeding of daylilies probably dates from about 1890. Previous to this all new types that had appeared in Europe and the United States were simply plant importations from the Orient. The development of new types from seedlings was begun about 1890 by George Yeld in England. His first introduction, named Apricot, appeared in 1892. A more recent contributor is A. B. Stout, of the New York Botanical Garden. He has attacked the breeding problem from a scientific angle, and it is to him that we owe the greatest part of the genetic information now available on this group of plants. The breeding of new forms has increased so rapidly, chiefly as a result of his research, that there are now probably more than 300 different varieties.

The breeding of daylilies is handicapped by many obstacles. Among these are self-sterility and cross-sterility, which inhibit seed setting, the hybrid nature of the available types, and the comparatively slow rate of increase after a desirable variety has been developed.

The types of sterility encountered may, according to Stout, be classified into four groups:

(1) There appears to be lack of affinity between certain species in the relations of fertilization. Yet hybrids have been obtained from many of the combinations between species.

(2) There is much abortion of pollen grains and egg cells in certain hybrids, such as *Hemerocallis flava* L. × *H. nana*, and in triploids, such as the Europa daylily. This condition greatly reduces the chance that a plant will bear seeds, but there may be a few viable pollen grains, in which case the plant may be used as a pollen parent.

(3) There is abortion of pistils in the older triploid double-flowered forms, although some viable pollen is formed.

(4) In daylilies there are many types of incompatibility. Some plants set seed only when self-pollinated, others when pollinated by sister plants, and still others only when cross-pollinated by certain other species. Studies have been made which show that in some cases of sterility pollen tubes grow poorly in the style or fail to enter the ovary. Some clones are completely self-sterile, others set a few seeds when self-pollinated.

The wide variation in any group of daylily seedlings is rather striking. Even seedlings of the older, well-established clones are usually very inferior to the parent type. This indicates, of course, that daylilies are probably heterozygous for a large number of genes. The chances of securing improved types depend almost entirely on the

number of seedlings grown. According to Stout, only 14 superior seedlings were found out of a total of 15,000 grown. Others apparently had some merit, since about 100 more were saved for use in selective breeding.

The present information on daylilies indicates that many new types can be developed by intercrossing the existing clones. Because of the heterozygous nature of the material, lack of genetic data, and general self-sterility, a scientifically planned breeding attack is difficult. About all that can be done at present is to grow large populations and select the superior types either for introduction or further breeding. It would be desirable to establish some self-fertile lines so that a genetic analysis of some plant characters could be made.

The cytological investigations of daylilies have shown some interesting results. The basic chromosome number of all the species appears to be 11. The common European form of *Hemerocallis fulva* L., which Stout calls Europa, has 33 chromosomes and is therefore a triploid. According to Belling and Stout this species shows considerable irregularity in the formation of pollen cells, so that very few good pollen grains or egg cells are formed. Further studies by Stout showed that triploidy was fairly common in daylilies and this may account for some of the prevalent sterility.

Iris

The garden irises may be grouped in several classes, such as the bearded, beardless, and bulbous types. This discussion is limited to the commonly cultivated tall bearded type. As is true of many other ornamental plants, the early history of the iris is shrouded in mystery. According to J. C. Wister, bearded irises are native to central and southern Europe and Asia Minor, in a region extending from the Alps through Italy, Hungary, Bulgaria, Palestine, and Iraq. There are no records of when man first began to cultivate the wild types, but it was probably very early, since the ancients attributed various medicinal properties to the rootstocks

Iris albicans Lange is the first species about the culture of which there is definite knowledge. This iris probably originated in Arabia and was carried all over southern Europe by the Mohammedans, who planted it on the graves of their soldiers. There are no records as to when this practice was begun, but by 750 A. D , when the Mohammedans were driven out of Spain, the species *albicans* was already well established there.

The first reference to the growing of the iris in European gardens was in 1790. At this time about a dozen wild forms were listed in several garden catalogs. The next 60 years saw a rapid increase in the popularity of irises, and it was during this period that the first iris breeding was begun. Prominent among the early workers were Lemoine, Jàcques, and Salter, who produced many new improved forms. Unfortunately there are no authentic records of what these three men did, and any varieties they may have named have been lost. The first authentic record of named iris seedlings was as recent as 1855. At this time M. Dauvesse, a nurseryman of Orleans, France, offered a half dozen or so new varieties.

Within a dozen years thereafter the growing of iris seedlings was undertaken by many people. The most prominent of these were

Louis Van Houtte and Verdier of France, Krelage, Roozen, and Van Leeuwen of the Netherlands, and Peter Barr of England.

Previous to 1890 it seems that most of the new seedlings were derived from the two species *Iris pallida* Lam. and *I. variegata* L. The results were limited by the potentialities of these two species. Sir Michael Foster about 1880 began collecting iris species and forms from all parts of the world to use in his breeding program. The results of some of his crosses were so striking that other breeders were stimulated, and soon a number of new species combinations began to appear. It is likely that errors of nomenclature may have crept into some of this early work, and there may be some doubt about the alleged parentage of some of the crosses.

Figure 18.—Grace Sturtevant, one of the leading iris breeders in the United States. Some of our finest iris varieties owe their origin to her.

Among the modern iris breeders of Europe, the late A. J. Bliss, of England, is probably the best known. He was interested in studying the relationships of many of the present varieties, but he also developed some very fine new ones. He did not specialize in one type of flower but was interested in a wide range of forms.

The history of iris breeding in the United States dates back to about 1905. At this time Bertrand H. Farr, of Pennsylvania, introduced a collection of superior new varieties from the English firm of Barr. Working with this material, he was able in 1909 to introduce some excellent new seedlings. This work soon stimulated widespread interest, and very shortly large numbers of amateur growers were producing seedlings. In an article of this length it is obviously impossible to mention all the American breeders.

One of the most careful and prolific workers is Grace Sturtevant, of Massachusetts (fig. 18). She has continuously maintained a collection of the very finest varieties to use as parent plants and has developed over 40 new worth-while introductions. Among them

Afterglow, B. Y. Morrison, Queen Caterina, Reverie, and Shekinah are of exceptional merit.

Another American breeder who developed some excellent new varieties was Edward B. Williamson, of Indiana. From about 1910 until his death in 1933 he introduced many new irises. One of the best known came from crossing about 500 flowers of the variety Amas with other varieties. Only one seed pod was formed in these crosses, and one of the seeds in it produced the seedling later named Lent A. Williamson.

J. C. Nicholls, Ithaca, N. Y., is credited with very careful work on iris breeding. He rigidly selects the parents for each cross and keeps a very careful set of records of all his work.

On the Pacific coast, the work of Sidney B. Mitchell and of E. O. Essig is noteworthy. Mitchell has developed many excellent new varieties and recently has devoted most of his time to development of new yellow types. Essig began iris breeding as a hobby and has carried on a series of careful experiments on seed germination under different conditions. He also has introduced several excellent new seedlings. Other American breeders of note are J. M. Shull, of Washington, D. C., and the Sass brothers, of Omaha, Nebr.

The methods employed by some of the better iris breeders are illustrative of the large amount of work necessary to produce really superior types. The late Edward B. Williamson formulated a plan to assure a higher degree of success with his crosses. From his early experiences he knew that many crosses would not produce seed, and the only way to discover which would was to attempt the cross. He decided to use a mixture of pollen in all crosses, reasoning that the prospect of getting some seed would be much better since there was a chance that one or more of the pollens used would be effective. The pollen was gathered from hundreds of flowers and mixed in a receptacle. From 1925 until his death in 1933 he planted each year from 70,000 to 100,000 seeds He never introduced more than 10 seedlings in any year. The percentage of worth-while varieties is thus rather low.

The methods of J. C. Nicholls are in decided contrast to those of Williamson. Accurate records of both parents are kept. Parents are selected with care, and about 3,000 seeds are planted each year. It is rarely the case that more than 1 iris worthy of varietal status is found in 1,000 seedlings.

Unfortunately little or nothing is known concerning inheritance in iris. Bliss made some preliminary observations on inheritance of leaf pigmentations and coloring of the beard, but the evidence is too meager as yet to warrant a genetic analysis of these characters.

The very early iris breeders simply planted seed and hoped something good would turn up. At the present time the better breeders choose both parents with care and control all crosses. This information about parental stocks, however, has little actual value unless the frequency of superior seedlings arising from each cross is known. Since many of the crosses give only a few seeds or none, a summation of data for the same cross from various breeders would certainly be

worth while. If such information were available a table of breeding qualities of various varieties could be made that would be of some value. Undoubtedly some of the more careful breeders have this sort of information on their own work, but it has not been collected and published.

According to the experience of some iris breeders, one of the serious problems has been sterility. Some varieties are both cross-sterile and self-sterile, others are cross-sterile and self-fertile, others cross-fertile and self-sterile, and still others both cross-fertile and self-fertile. In some cases there are differences of opinion concerning certain varieties, which indicate either an error in nomenclature or that the same variety behaves differently in various localities. In general it can be said that crosses between closely related types have the best prospect of producing seed, with less and less success as the varieties are more distantly related. Likewise, hybrids between closely related types are most likely to be fertile.

Another difficulty is slow and sometimes poor seed germination. To a geneticist attempting to work on the inheritance of some character this is a great obstacle. Whether or not it is due in some cases to poor horticultural practice, it is one of the things that will have to be overcome before much real genetic research can be accomplished.

Lily

To many people in the United States the word lily is closely associated with thoughts of Easter, and they are familiar with only the large-flowered, so-called Easter lily, *Lilium longiflorum* Thunb. This lily is widely grown by florists, who force it for sale as potted plants and also as cut flowers. Easter lilies are rarely grown in outdoor gardens except in very mild climates where they are able to survive the winters and are not exposed to late spring frosts.

One of the best known of the other lilies is the popular so-called Tiger lily, *Lilium tigrinum* Ker. This old-fashioned favorite is a very hardy species and has become widely distributed throughout most parts of the country. Not long after it was introduced from China it escaped from cultivation and is now found growing wild in many sections.

Table 2.—*Species of Lilium classified according to date described and continent of origin*

[Compiled from Stoker (*494*)]

When described	Species originating in—			Total	When described	Species originating in—			Total
	North America	Europe	Asia			North America	Europe	Asia	
	Number	*Number*	*Number*			*Number*	*Number*	*Number*	
1753	1	5	[1] 1	6	1876–1900	5	2	11	18
1754–1800	3	1	3	7	1901–25	4	2	13	19
1801–25	1	1	5	7	1926–36	1	0	5	6
1826–50	0	3	5	8					
1851–75	7	0	6	13	Total	22	14	49	84

[1] Duplicate.

Until very recently only a few lily enthusiasts were familiar with the many beautiful garden forms now available. Most of these new types are wild species from afar that have been introduced by plant explorers. Asia has furnished nearly two-thirds of these, as is shown in table 2. Until quite recently the species introduced by plant explorers more than met demands for new types. The prospect of finding striking and distinct new forms in the wild is now rapidly diminishing, for they do not readily escape the eye of the botanical explorer. Since this is true, it seems that in the future new and superior lilies must come from the plant breeder rather than the explorer.

As recently as 50 years ago only a dozen species of *Lilium* were grown in England, and few sources of bulbs or seeds were available to enthusiasts who wished to grow others. At the turn of the century interest in lilies was waning, but was revived by the introduction of the easily grown *Lilium regale* Wils. from China in 1904. Other new forms from China followed, including *L. sargentiae* Wils. and *L. willmottiae* Wils. The formation of a lily committee by the Royal Horticultural Society and publication of its Lily Yearbook, beginning with 1932, also stimulated interest in England. In the United States the popularity of lilies has kept pace with the growing interest in flowers in general, and the American Horticultural Society has appointed a lily committee this year (1937). New hybrids and more readily available stocks of lily species have also encouraged wider use in gardens everywhere.

A uniform system of naming lilies is essential to an intelligent discussion of lily breeding. Unfortunately for the general public only a few species have well-recognized common names. The use of botanical names is general even in popular accounts, and while these may have a forbidding technical appearance, yet they are in most instances the only generally accepted designations available. For example, the popular Regal lily is known to all botanists and lily enthusiasts as *Lilium regale*. Since most lily breeders become interested in the relationships of the various forms, an outline of the division of the genus *Lilium* into subgenera and sections has been included in the appendix. In this appendix also is a list of lily hybrids, including reports of species crosses from which no named hybrids have been grown. Such a list should be helpful to the amateur hybridizer in pointing out which crosses are readily made and which combinations are difficult or not yet accomplished.

On this continent notable contributions to our array of garden lilies have been made by the late David Griffiths (fig. 19), of the Department, and by Isabella Preston, of the Dominion Experimental Farm at Ottawa, Canada. Griffiths is best known for his work on the propagation of lilies, but he developed and distributed a number of fine Martagon hybrids (*152*), one of which is Star of Oregon. Miss Preston has made great numbers of cross-pollinations with the principal objective of developing hardier lilies for Canadian gardens. Some of her named productions are George C. Creelman, Davmottiae, and the more recent Grace Marshall, Lila McCann, Lilian Cummings, and Phyllis Cox. Many amateurs are active in the United States and in Canada, and some fine hybrids have resulted from their efforts.

In England the Backhouse hybrids produced by Mrs. R. O. Backhouse of narcissus fame are perhaps the best known of the newer lilies, but activity is widespread there as well as on the Continent of Europe.

In the literature of lilies the notation of hybrids has been so casual that Miss Preston felt it desirable to state: "In my notes the seed parent is placed first" (*410*). Other writers have departed from this practice so commonly that it is only by chance reference to one or the other species as seed parent or pollen parent that the reader can tell which cross is discussed. It should also be pointed out that some reported hybrids are based on inferences as to what the parents should have been to produce the observed effects, and, further, that some reported hybrids may be merely asexual offspring of the seed parent. Natural hybrids are not common in *Lilium*, at least in England, according to Grove (*155*); but Preston (*410*) reports two from Canada. *Lilium testaceum* Lindl., *L. elegans* Thunb. (syn. *L. thunbergianum* Schultes), and *L. umbellatum* Hort. are all recognized as hybrids of long standing, in the origin of which man may have played no part.

Figure 19.—The late David Griffiths (1867–1935), who did outstanding breeding work on lilies and narcissus while a member of the United States Department of Agriculture. He is also well known for his work on methods of propagation and production of tulips and hyacinths.

Several examples of supposedly hybrid seedlings that appeared to be identical with the maternal parent were recorded by Parkman (*402*) in 1878. He found that *Lilium superbum* L., emasculated and pollinated by *L. auratum* Lindl., *L. tigrinum* Ker, *L. chalcedonicum* L., or various other species, produced seedlings that were always pure *L. superbum*. When these seedlings were pollinated with other species, the second generation was still unchanged *L. superbum*. Similar results followed the application of pollen of other species to *L. umbellatum* Hort., and the Easter lily, *L. longiflorum*. Griffiths has commented that maternal inheritance is remarkably prevalent in lilies, and (*154*) that *L. regale* yields better results when used as a pollen parent because of this tendency. Stout (*497*) concedes that seedlings of maternal character in *Lilium* may result from wide crosses, without fertilization and production of true seeds. Preston (*409*) has found that seedlings of *L. regale* pollinated with *L. speciosum* Thunb. var. *rubrum* Hort. or with *L. longiflorum* are strictly maternal in character, and that the progeny of a *L. regale* × *longiflorum* cross remained pure *L. regale* in the second generation.

Further reports of similar nature could be cited. Such results might be attributed to late or incomplete emasculation or to ineffective protection against pollen of the maternal species, but such explanations cannot be pressed in the face of reports from careful hybridizers. Some form of parthenogenesis must be assumed in the production of such pseudohybrids, as is suggested by Hall and his coworkers (*191*):

> The possibility has to be borne in mind that crossing certain lilies may not result in producing true seed, i. e., by sexual union of the pollen cell with ovule. Excitation due to the foreign pollen may induce the formation from the ovule of a "seed" which is really a bud of the mother plant into which the pollen has not entered.

It has already been mentioned that many hybrid lily types of the past century in particular were noted alike for their beauty and their quick disappearance. Striking examples are Parkman's *Lilium speciosum* × *auratum* (1869) and the reciprocal cross produced by Hovey about 1880, each of which persisted scarcely long enough to be admired and photographed. Most of Burbank's productions are now only memories.

Premature passing of some hybrid types is clearly due to misfortunes of culture before the stock was developed to commercial quantity. It was Griffiths' aim to stress the need for rapid, efficient vegetative propagation to insure establishment of a desirable hybrid as soon as possible, and he devoted much of his energy to improving methods of propagation with this in mind. Some desirable hybrids are inherently slow or difficult to propagate (*151*) and may be lost through the producer's haste to market his creation. Other hybrids, of course, are genetically weak and incapable of long survival, an extreme example of which is the albino seedling.

One of the least excusable reasons for loss of a hybrid is failure to recognize the necessity of vegetative propagation if the stock is to be kept true to type. Very frequently seed of a promising hybrid lily is offered for sale and the seedlings produced are sometimes called by the name of the parent plant. This is obviously a wrong procedure, since it would be very unusual for a first-generation hybrid to breed true. Griffiths (*151*) also calls attention to the fact that there has been a tendency to treat all the hybrids coming from a cross as a variety rather than selecting an outstanding one for vegetative increase as a clonal variety. Such practices have undoubtedly added to the present confusion regarding many named lily hybrids. They are contrary to the fundamental principles of genetics, and lily breeders will do well to discard them.

Another important reason for decline or loss of lily hybrid varieties is the presence of virus diseases such as mosaic (*155*). The viruses are carried in the living cells of the plant and are spread from plant to plant by aphids. When a diseased lily is propagated by division, by stem bulblets, or by scaling, each new plant produced will have the disease. No method is known by which such diseased lilies can be made healthy. If a new hybrid is attacked, it may as well be discarded. Fortunately these diseases are not commonly transmitted through the seed. Accordingly seedling lilies are usually free from virus diseases to begin with and should be grown at a safe distance from affected parent plants and other diseased lilies.

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It is generally known that some species of *Lilium* do not readily set seed when pollinated with their own pollen. As early as 1890, Focke demonstrated that *Lilium bulbiferum* L. could be divided into certain groups which would set seed only when pollen was used from a member of another group (*497*). There are many references to the failure of the Madonna lily (*L. candidum* L.) and the Tiger lily (*L. tigrinum*) to develop seeds. Preston states that *L. testaceum* and *L. hansoni* Leichtl., as well as *L. tigrinum*, are self-sterile at Ottawa, Canada. She later (*410, 411*) reports a fertile strain of *L. tigrinum* that she has named "var. diploid." Griffiths cites *L. regale* and *L. longiflorum* as species that set seed only when different plants are interpollinated. Amsler (*4*) reported that *L. brownii* Poit. and *L. parryi* S. Wats. set no seed when selfed, but did when pollinated with other strains of the same species. Stout (*497*) and others who have studied self-incompatibility in *Lilium* made systematic trials with proper attention to emasculation, bagging, and hand pollination, and showed that failure of individual plants to set seed on selfing is widespread in lilies. *L. tigrinum* and its varieties *flore-pleno, splendens,* and *fortunei* are triploids (*191*), having 36 chromosomes, and rarely mature functional sex cells. The "variety diploid", however, has the normal diploid number of 24 chromosomes and is self-fertile (*497*). In other species the failure to set seed is not due to inability to develop functional gametes, as is shown by the successful results of interpollinating different lines within a species. Even the triploid *L. tigrinum* will sometimes set seed with the pollen of *L. leichtlini* var. *maximowiczi* (Regel) Baker.

Stout (*497*) mentions occasional instances of failure of lilies to form functional pistils or stamens. He also found poorly formed, nonfunctional pollen in the hybrid *L. testaceum*, which he explained as caused by hybridity and a like condition caused by triploidy in *L. tigrinum*, but he holds that incompatibility is the most important reason for failure to set seed in *Lilium*. In the species *L. henryi* Baker, *L. speciosum* Thunb., *L. superbum*, *L. elegans* Thunb., *L. bulbiferum* subsp. *croceum* (Chaix) Baker, *L. dauricum* Ker, *L. philadelphicum* L., *L. auratum* Lindl., *L. humboldtii* Roezl and Leichtl., *L. kelloggii* Purdy, *L. willmottiae*, *L. roezli* Regel, *L. longiflorum*, he found self-sterility to be the rule but some few individuals set a little seed with their own pollen. Among 59 plants of the common wild lily, *L. canadense* L., 4 fully self-fertile individuals were found, 6 partially self-fertile and 49 wholly self-sterile. Interpollinations of self-sterile plants were successful in nearly all cases. Over 100 plants of *L. hansoni* studied were fully self- and cross-sterile and may represent a single clone. This strain was, however, reciprocally fertile with a new strain of *L. hansoni* received from Manchuria. Stout found no fully self-fertile individuals in *L. candidum*, and cross-fertility was rare and partial until a new stock of unknown source was encountered. Species in which Stout found no self-fertile individuals are *L. hansoni*, *L. candidum*, *L. tigrinum* (excluding the "variety diploid"), *L. parryi*, *L. chalcedonicum* L., *L. brownii*, *L. grayi* S. Wats., *L. sutchuenense* Franch., and *L. maximowiczii* Regel (= *L. leichtlini* var. *maximowiczii*).

Now that the pitfalls of the past are better understood, lily breeding is undoubtedly on a surer basis and prospects are brighter than ever before. The importance of vegetative propagation of hybrids is

becoming recognized, and the methods of vegetative reproduction have been improved. All hybrids start as seedlings and are, therefore, usually free at first from virus diseases, since, as pointed out earlier, these diseases are not commonly seed-borne. This point has become widely appreciated, and efforts are being made to grow as many lilies as possible from seed. When mosaic-free stocks of garden lilies are more generally available, the prospects of increasing a hybrid clone to commercial proportions before it becomes affected will be greatly enhanced.

Some of the possibilities of hybrid combinations may be seen from the tabulation of reported hybrids in the appendix. Crosses are in general more successful within one section of the genus, but a number of successful combinations of Archelirion with Martagon and of Leucolirion with Martagon (see the appendix) are on record. Combinations not yet accomplished may succeed for the persistent breeder. Cytology reveals no discouraging differences in chromosome numbers, except in the case of the triploid *Lilium tigrinum.*

Some of the specific objectives of hybridizers are extension of the flowering season (*155*), extension of the color range in reliable garden forms (*151*, *155*, *410*), development of garden types even hardier than *Lilium regale* (*410*), and incorporation of superior vigor and adaptability in difficult garden subjects, such as *L. leichtlinii* Hook. f. (*155*), *L. humboldtii* (*153*), and others (*151*). Griffiths suggests *L. henryi* Baker as a promising parent carrying vigor and apparent tolerance to diseases.

Unfortunately, little is known concerning inheritance in lilies. Some of the species that are self-fertile do not give uniform seedlings, which indicates that they themselves are hybrids. This situation is to be expected because of the widespread self-sterility existing in the genus which makes cross-pollination necessary for seed setting.

Nasturtium

The native home of the nasturtiums (*Tropaeolum* spp.) seems to be the western coast of South America. They were found there by the early Spanish explorers and introduced by them to Europe from Peru. This probably happened sometime in the latter part of the sixteenth century. The two species that found favor in Spain were *T. minus* L. and *T. majus* L. From Spain they soon spread over most of Europe. In England they were known as "Indian Cresses", the name Indian being used because they came from the Spanish colonies in South America, which at that time were described as the Indies. At first the smaller-flowered *T. minus* was the most widely grown, but on the introduction of varieties of the larger-flowered *T. majus*, the small species was soon neglected. At the present time both types are found growing wild in many sections along the west coast of South America. The two species cross very readily, and many of the so-called Tom Thumb varieties are supposed to have originated in this manner.

The range of colors and color patterns in the modern nasturtium is one of the widest in the flower kingdom. In addition, some varieties are known to bear flowers of various shades on the same plant. The number of varieties listed today is very large, practically all having been developed by professional and amateur efforts.

Not much is known as to the inheritance of flower color. Rasmuson (*427*) has done some work and reports dark yellow as dominant to light yellow, and presence of red to its absence. He also crossed varieties bearing variegated flowers with some nonvariegated flower types. From these crosses he was able to determine that variegation was dominant. In the same investigations it was shown that the dark green color of the leaf was determined by two genes, green being dominant to yellowish green, and both to variegated.

In habit of growth the nasturtium may be divided roughly into three types—the tall or climbing, the bush, and the dwarf bush. When a cross is made between a pure tall and a bush, all the hybrids are tall, and in the next generation there is a ratio of 3 tall to 1 bush. This, of course, shows that climbing is dominant and controlled by a single gene.

Recently considerable interest has been aroused by the introduction of a double form which was named Golden Gleam (fig. 20). The origin of this variety is something of a mystery. It was found about 10 years ago by J. C. Bodger in a flower garden near El Monte, Calif. According to the owner, the seed had been brought into California from Mexico, where it had been introduced from Spain. A search for the type in Mexico, especially in the locality where it was reported, was unsuccessful.

The seed from the California plant was sown the next year and all seedlings proved to be doubles and true also for color. Within a few years the seed was increased to considerable quantities and the new variety introduced. Since other double-flowering plants of the same type were not found, it seems that Golden Gleam probably arose as a mutation from a single-flowered variety. There have been other double nasturtiums, however, one being known as early as 1730, when it was described and figured in colors in the Catalogus Plantarum. The horticultural flore-pleno type mentioned in Bailey's Cyclopedia is probably the same thing. This type, which is still grown to some extent in Europe, differs considerably from Golden Gleam. It is supposed to be entirely double, without production of pollen. Golden Gleam, on the other hand, has anthers and a pistil and sets seed.

Shortly after the discovery of Golden Gleam, cross-pollinations were made to develop other colors. This work was undertaken by Bodger and Burpee. As a result, several mixtures of colors and a scarlet double form appeared on the market a few years ago.

The inheritance of doubleness in nasturtiums has recently been worked out by Eyster and Burpee (*125*). According to these workers, singleness is a simple dominant to doubleness. When a pure single variety is crossed with a double, all the hybrids are single. In the second hybrid generation from such a cross, 78 plants were single and 27 double. This is very nearly a perfect 3:1 ratio. Since it is such a simple situation, we may expect to have all colors represented in the double type in a very few years.

A second double nasturtium has also appeared quite recently. It differs very markedly from both the Golden Gleam type and the earlier double reported from Europe. In the single flower there are five petals while, according to Eyster and Burpee, Golden Gleam varies from an occasional 5-petaled to a 15-petaled flower. The mean petal number

Figure 20.—The double-flowered nasturtium Golden Gleam. This variety was found growing in a garden at El Monte, Calif. It was reputed to have come from Mexico, but a diligent search in that country failed to locate any plants or information regarding it. (Courtesy of Bodger Seeds, Ltd.)

seems to be slightly under 10. The new double type, which is called superdouble, has from 40 to 50 petals, no pistil, and several modified stamens. It does form some good pollen, so it may be regarded as a staminate flower.

The origin of this new extreme double seems to have been spontaneous. It was first noticed in a greenhouse of several thousand double-flowered plants. Since it lacked pistils it could not set seed and had to be propagated by cuttings. The presence of some pollen, however, made it possible to use it as a male parent in crosses with singles and with doubles of the Golden Gleam type. When it was crossed with pure single plants, about half the hybrids were singles and about half superdoubles. Likewise, when crossed with Golden Gleam a 1:1 ratio of doubles and superdoubles was secured. From these results it is apparent that the new superdoubles are all heterozygous (impure) for the new character, which is obviously a simple dominant to both singleness and doubleness. If they had been homozygous (pure), all the hybrids would have been superdoubles in both instances. From this it can be seen that the production of new colors in superdoubles involves an actual hybridizing process. They can be made only by crossing a superdouble with a single or double of some new color. If the gene for superdoubleness is not in the same chromosome as the gene or genes for color, it will be a comparatively simple matter to provide the extreme double in the full color range of the ordinary single nasturtium. If the color gene and the superdouble gene are in the same chromosome the desired result can still be secured, but it will require the growing of a much larger population in order to get the new combination. Unfortunately, adequate linkage data are not available for nasturtiums.

Rose

The rose is one of the most widely grown and admired of all the flowers. There now exist several thousand named varieties in a wide range of color and form, including types for almost all conceivable conditions of growth. The greenhouse forcing roses, hardy outdoor varieties, climbers, bush, and polyanthas are some of the many types now grown. This wide variation and development has largely occurred in comparatively recent years.

The rose is one of the oldest of our cultivated flowers. It first appears in the early art of long-destroyed civilizations and is frequently mentioned in the Bible and in Greek mythology. It was undoubtedly the favorite flower of many of the rulers of Greece and Rome and was used as a symbol on their banners and shields. This early popularity continued on down through the Middle Ages, and roses were the symbols for the great houses of York and Lancaster in the so-called Wars of the Roses in England.

The genus *Rosa* is a large one with several races, widely distributed, and native mostly in the North Temperate Zone. However, a few species are found near the Equator and even above the Arctic Circle. Many of the finest are native to eastern Asia, but they have not been so highly developed there as in the western part, especially about the eastern end of the Mediterranean Sea.

In Europe during the sixteenth century only a few rose varieties were cultivated and at least half were singles. Two hundred years later there had been only a slight increase in the available varieties. In England at this time there were 21 species in cultivation, and about 30 double varieties. Importations were very rapid after 1789. In this year the Crimson Chinese Monthly, *Rosa chinensis* var. *semperflorens* Koehne, was introduced. Three years later the Macartney, *R. bracteata* Wendl., made its first appearance, and in 1796 *R. rugosa* Thunb. This was followed by *R. multiflora* var. *carnea* Thory, the first rambler rose, in 1804; *R. banksiae* R. Br., in 1807; *R. chinensis* var. *odoratissima* Lindl., the tea-scented rose, in 1809; and the Fairy rose, *R. chinensis* var. *minima* Rehd., and Eduard, a Bourbon type, in 1810. About 1816 a rambler rose, Seven Sisters, *R. multiflora* var. *platyphylla* Thory, appeared. This was followed in 1823 by the microphylla or small-leaved type, *R. roxburghii* Tratt., from China. While only meager records are available, it seems very probable that these new species were used in crosses with some of the native species such as *R. gallica* L., *R. rubiginosa* L., and the so-called Ayrshire roses. By 1829 R. Desportes briefly described 2,562 species or varieties then under cultivation in France. This enormous increase in so short a period is very interesting. It is extremely improbable that it was in any way caused by a sudden tendency to production of sports or mutations. Other factors are more likely to have been responsible, among which importation from other continents and the growing and selection of seedlings were probably two of the most important.

Cultivated roses were probably brought into the United States by the earliest colonists. Very little is known concerning them during these early days, and it was not until after the Revolutionary War that any account is found of the naming of a new variety. This rose, called Mary Washington, may very well be the first truly American production. Shortly following this the Champney or Noisette roses were developed, and soon after, in 1840, Feast Bros., of Baltimore, introduced hardy climbers having our native *Rosa setigera* Michx. as one parent.

At the beginning of this century, most of the rose varieties grown in the United States had originated in Europe. These importations were very frequently disappointing in their behavior, and it was soon realized that varieties should be developed under local environmental conditions. This situation stimulated the efforts of American rose breeders, and today there are hundreds actively engaged in this fascinating work. In an article of this length it is obviously impossible to cover all the contributions of these workers.

One of the earlier pioneers in the breeding of modern roses was the late E. G. Hill, of Richmond, Ind. His first activity with roses began in 1851 when he was employed in the nursery of T. C. Maxwell & Bros. at Geneva, N. Y., where he became familiar with the very best varieties then available. In 1865 the Hill family moved to Richmond, Ind., and in 1881 father and son launched the well-known firm of E. G. Hill. About 1891 Hill began importing the newer hybrid teas to test for cut-flower production under American conditions, and during this last decade of the past century he undertook his own breeding work. It was not until 1904 that two roses resulted which he believed

were superior. These were General MacArthur and Mrs. Theodore Roosevelt. In 1905 Richmond was selected from a large group of red seedlings. These popular varieties were followed by many others.

Another American breeder who introduced many well-known varieties is John Cook, of Baltimore. His first successful hybrid, Souvenir of Wootton, was introduced in 1888. Other well-known varieties developed by him are My Maryland, Radiance, Panama, and Francis Scott Key.

Alexander W. Montgomery, Jr., of Hadley, Mass., is another who has contributed valuable new varieties. Two of his introductions, Hadley and Mrs. Charles Russell, are still very popular. The Dorners, in La Fayette, Ind., have also produced several valuable roses. Probably the best known of these is the widely grown Hoosier Beauty.

The methods used by most of the amateur and professional rose breeders are probably very similar. In general, some ideal type is determined upon and the breeder attempts to secure it by crossing two varieties, each possessing some of the desirable characters. In many instances, the eventual result is far different from the predetermined ideal, in fact, may even surpass it. In general, only a few really successful new roses occur in a population of several thousand seedlings. As an illustration of the odds against securing a really desirable new seedling when varieties are crossed, the following is quoted from an article by Hill (*206*) in the American Rose Annual for 1917:

> From the 1914 crosses there were germinated over 2,500 seeds. Each little plant was given special culture, being planted in a bench where it received the same care as that required by the most important forcing varieties. In 1915 the first weeding out of the seedlings occurred, and by 1916 the 2,500 seedlings had been reduced to about 800. These were tested in blocks of five, receiving the most rigid attention and critical scrutiny.
>
> By the opening of 1917, the seedlings have been reduced to some fifteen sorts which Mr. Hill considers worth while going farther with. Of these fifteen several have been selected, named and registered, and propagation is proceeding with the idea of later dissemination.

From this group of 15 came: (1) Columbia, resulting from the cross Ophelia × Mrs. Shawyer; (2) Double Ophelia, from a cross between Ophelia and an unnamed seedling variety; (3) Rose Premier, from a cross between Ophelia and Mrs. Charles Russell; and (4) Mary Hill, from a cross between Ophelia and Sunburst.

Again quoting:

> Others of the fifteen sorts are full of promise and will be reported upon later. It may be observed that all of these roses are selected primarily from the forcing or commercial cut-flower standpoint, but it is by no means improbable that several of them may also prove as fine for outdoor use as General MacArthur.

A careful study of these results is very interesting. Suppose all 15 surviving seedlings are finally selected as worth while. The ratio of the total seedlings to the number of good ones is then 2,500:15, or about 1 desirable in 166. It is very probable that the ratio is often considerably greater than this, in some instances reaching odds of over 1,000 to 1.

The very wide variability exhibited by a large group of rose seedlings has been a constant puzzle to many rose breeders. As early as 1889

Lord Penzance, a prominent English rose breeder, published the following statement: "Roses of the first order are, after all, very rare in a sowing of seed, and their production is a veritable lottery, in which chance plays the principal part."

Until fairly recent years, most rose breeders did not even keep a record of parent varieties used in a cross. The lack of this information has been deplored by many observers, but it is doubtful whether such data would have the value apparently attached to it. For instance, the parentage of the widely-grown old favorite, Caroline Testout, is well-known, but it is very doubtful whether any breeder could repeat the cross and secure another Caroline Testout. It is not meant that such a result is impossible, but it is improbable. It might occur if a very large number of hybrid seedlings were grown. There is, however, a possible value in knowing the parentage of rose varieties. It is very probable that we should find certain varieties more apt to produce successful offspring than others. Such information might be helpful in planning cross-pollinations.

The extremely mixed heredity of rose varieties makes planned breeding very difficult. Since propagation is easily accomplished by budding and grafting, this heterozygous condition is not a handicap to the rapid increase of any variety.

TABLE 3.—*Roses developed by Walter Van Fleet*

Year	Variety	Type [1]	Parentage
1895	May Queen	H. W.	*Rosa wichuraiana* × Mrs. de Graw.
1895	Ruby Queen	H. W.	Queen's Scarlet × *R. wichuraiana*.
1895	Clara Barton	H.T.Poly.	Clothilde Soupert × American Beauty.
1895	Alba rubrifolia	H. W.	*R. wichuraiana* × Coquette de Lyon.
1900	Magnafrano	H. T.	Magna Charta × Safrano.
1895	Pearl Queen	H. W.	*R. wichuraiana* × Mrs. de Graw.
1900	New Century	H. R.	*R. rugosa alba* × Clothilde Soupert.
1902	Philadelphia	H. M.	Crimson Rambler × Victor Hugo.
1903	Beauty of Rosemawr	Bour.	
1898	Northern Light	H W.	
1900	Sir Thomas Lipton	H. R.	*R. rugosa alba* × Clothilde Soupert.
1904	Charles Wagner	H. P.	Jean Liabaud × Victor Hugo.
1902	American Pillar	H. W.	(*R. wichuraiana* × *R. setigera*) × a red hybrid perpetual.
1900	Birdie Blye	H. M.	Helene × Bon Silene.
1905	Rugosa magnifica	H. R.	*R. rugosa* × Ard's Rover.
1907	Garnet Climber	H. W.	*R. wichuraiana* × Lucullus.
1899	Dr. W. Van Fleet	H. W.	(*R. wichuraiana* × Safrano) × Souv. de Pres Carnot.
1908	Silver Moon	H. W.	(*R. wichuraiana* × Devoniensis) × *R. laevigata*.
1902	Mary Lovett	H. W.	*R. wichuraiana* × Kaiserin Augusta Victoria.
1902	Bess Lovett	H. W.	
1902	Alida Lovett	H. W.	*R. wichuraiana* × Souv de Pres. Carnot.
1918	Aunt Harriet	H W.	Appoline × *R. wichuraiana*.
1921	Mary Wallace	H. W.	*R. wichuraiana* × hybrid tea.
1923	Heart of Gold	H. W.	(*R. wichuraiana* × *R. setigera*) × *R. moyesi*.
1925	Sarah Van Fleet	H. R.	*R. rugosa* × a hybrid tea, possibly My Maryland
1925	Dr. E. M. Mills	H. R.	
1926	Breeze Hill	H. W.	*R. wichuraiana* × Beaute de Lyon.
1926	Glenn Dale	H. W.	*R. wichuraiana* × Isabella Sprunt.
1927	Ruskin	H. R.	*R. rugosa*, Souv. de Pierre Leperdrieux × Victor Hugo.

[1] Abbreviations have been used to designate the class to which the rose belongs:

H. W.=Hybrid wichuraiana.
H. R.=Hybrid rugosa.
H. T.=Hybrid tea.
H. T.Poly=Baby rambler with hybrid tea characteristics.
H. M.=Hybrid multiflora.
H. P.=Hybrid perpetual.
Bour.=Bourbon.

While American rose breeders were not at first so active as Europeans in producing hybrid teas, they have accomplished much in developing hardy outdoor roses. One of the leaders in this work was

the late W. Van Fleet (fig. 21), who continued his rose-breeding activities after he became a member of the Department of Agriculture. He was an industrious worker, making many thousands of crosses and keeping accurate records of his work. His objective was to produce continuous blooming roses for common dooryard culture under the diverse climatic conditions of this country. In order to develop such types he utilized all available vigorous species of pleasing aspect, as well as strong-growing garden forms, crossing them with highly developed florists' varieties. In this manner he hoped to secure plants that would combine the really desirable characters of the parents. Two varieties developed by him were introduced posthumously.

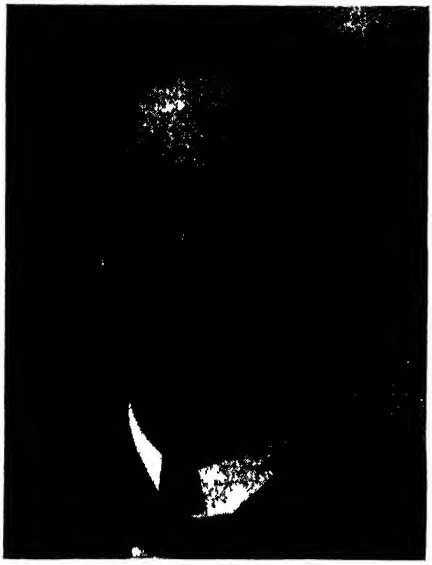

Figure 21.—The late Walter Van Fleet (1857–1922), of the United States Department of Agriculture, who did outstanding work on breeding hardy outdoor roses. He set as his goal the development of hardy dooryard roses that would bloom continuously from early spring until frost.

The complete list of Dr. Van Fleet's varieties is given in table 3, where they are arranged in the order of their introduction. It is interesting to note how few species entered into the formation of these varieties. Thirteen of the nineteen had *Rosa wichuraiana* Crépin as one parent; three had *R. rugosa*, two *R. setigera*, one *R. multiflora* Thunb., and one *R. moyesi* Hemsl. and Wilson. Some of these introductions have gained widespread recognition and are widely grown.

Another breeder of hardy roses is N. E. Hansen, of the South Dakota Agricultural Experiment Station at Brookings. He has been working for some time to develop roses to withstand the severe winters of that section. His first introduction was the variety Tetonkaha, which appeared in 1912. In 1926 a second variety, Tegala, was released, and in 1927, 13 others were introduced. All these varieties have proved hardy at the Brookings station and have been distributed in the Northwest prairie region.

The great diversity of form and habit in any group of rose hybrids is easily understood. To the geneticist it is the naturally expected outcome when two highly heterozygous plants are cross-pollinated. While the records of early hybridization in roses are none too authentic, they do at least show that the ancestry of our modern varieties is very complex. Thus the hybrid teas probably originated from a cross between a hybrid perpetual and a tea rose. The teas are supposed to have come from *Rosa odorata* Sweet. The hybrid perpetuals have a very complex ancestry. As far as can be determined, the earliest progenitor was a damask rose called The Four Seasons.

It was being grown commercially in 1790 and was probably crossed extensively with the French and Provence roses to give rise to the damask perpetual. It seems that these were then crossed with China roses, from which came the hybrid China types. According to the records of this period all roses in this last group were apparently sterile, but in 1830 a M. Guerin produced a hybrid named Malton, which proved to be fertile. A second fertile hybrid called Athalin was produced the same year by Jacques, gardener to the King, at Neuilly. It is very likely the damask parent of each was a descendant from the variety The Four Seasons. A few years later the variety Athalin was crossed with Rose du Roi, a damask perpetual. Some of these crosses were called hybrid damasks and were the direct forerunners of the hybrid perpetuals. In 1837, M. Laffay, a florist located at Bellevue, near Paris, introduced Prince Albert and Princess Helene, two new varieties. They were of the hybrid-perpetual type, and M. Laffay is usually credited as the originator of this group. He later produced other varieties, among which was La Reine. In 1844, groups of hybrid Chinas, bourbon perpetuals, hybrid damask perpetuals, hybrid Gallicas, and moss roses were all combined to form the hybrid perpetual group.

The hybrid teas, then, have a very diverse ancestry. This complexity has been greatly multiplied by crosses among themselves, so that our modern hybrid-tea varieties are undoubtedly a conglomeration of many ancestral characters. Is it any wonder that even in a group of thousands of hybrids from seed, no two are exactly alike?

The sudden spontaneous appearance of so-called sports in roses is a well-known phenomenon. The frequency with which they appear is not known, although some varieties are supposed to produce more than others. This, however, is probably based on the limited numbers considered worthy of introduction rather than on the total actually produced. There is little information about such sudden changes in parts of the plant other than flowers. In many instances the sport involves only a slight change in flower color, although very sharp breaks, such as from red to white, are also known.

These mutations in the hereditary material in the cells may occur at different stages of development and in different parts of the plant. When, for instance, a red rose produces a branch bearing white flowers, doubtless a change has occurred in the petal cells that carry the color pigments. The change may have occurred in the bud that produced the side branch, or it may have occurred at any time during the growth of the shoot and flower bud. Sometimes the change in hereditary material comes after the flower bud is almost fully developed. In such instances we may have bicolored flowers, each pigment being restricted to a very definite sector.

It may sometimes happen that a particular bud taken from a mutated branch fails to produce the new flower type. Such a situation is called a reversion by rose breeders, but it probably indicates that the mutation occurred after this bud had been formed.

No one as yet has been able to induce a sport in roses or explain the forces that bring about the change under natural conditions. Some of the future research on roses will undoubtedly be concerned with such matters. It is possible that exposure of buds to X-rays, radium,

heat, or some chemical might induce radical changes. Until such time one must depend on the chance occurrence of mutations. Unfortunately the erroneous idea has become current that special credit is due the introducer of a new rose sport. Actually the rose breeder has no control whatever over its appearance. He is simply fortunate in having the mutation occur in one of his plants. Such introductions should not be classed with actual breeding work where planned cross-pollinations are made and thousands of seedlings grown. Even in the latter case, our present methods are very little advanced over what they were 45 years ago, when Lord Penzance called rose breeding a lottery.

The contributions of science to rose breeding have been concerned chiefly with pollen studies, studies of the chromosomes of the various species, and methods of hastening seed germination. The classification of the genus *Rosa* into species has been a very difficult problem. Various workers have from time to time revised the classification, and there has not been any general agreement among them. This confusion is probably caused by the lack of agreement on what constitutes a species, as well as by the undoubted heterogeneous nature of roses. In early days, as well as now, natural crosses between wild roses probably occurred, giving rise to new intermediate forms. When rose growing became so popular, amateurs began making cross-pollinations between all available types, thus further complicating the situation.

At the present time most rose varieties and so-called species are actually mixtures of many types. Classification as botanical species is practically impossible. Undoubtedly many of our present so-called species are simply hybrids, as is indicated by the degrees of partial sterility found.

An interesting study of the pollen of several wild species and some species hybrids was made by Erlanson (*120*). Her method consisted in staining the pollen and counting the percentage of poor, shriveled grains. She found that poor pollen exists in all our native American rose species. It averaged about 20 percent infertile in all except *Rosa acicularis* Lindl. and *R. palustris* Marsh., where it was about 10 percent. Even relatively fertile individual plants had as much as 25 percent infertile pollen. In hybrids the percentage of poor pollen was usually very much greater than in the wild species, and the conclusion was reached that any wild rose plant with over 70 percent of infertile pollen and setting little or no fruit was probably a first-generation hybrid.

Observations of the chromosomes of roses have also thrown some light on the species problem. Rose species have been found with 14, 21, 28, 35, 42, 49, and 56 chromosomes in the body cells. These numbers increase each time by 7 and are called a polyploid series. According to Hurst there are distinctly different seven-chromosome groups. He assumes at least five such groups, which he designates as A, B, C, D, E. Different combinations of these five chromosome sets would certainly explain much of the wide variability in the genus.

One of the greatest handicaps faced by rose breeders is the matter of irregular seed germination. Seed from some species sprouts readily, while that from others may not start growth for several years. In

1926 William Crocker, of the Boyce Thompson Institute at Yonkers, N. Y., published results of his studies on after-ripening and germination of rose seeds. The seeds were stored at various temperatures in moist granulated peat. The best temperature for both species and hybrids was found to be 41° F. In some cases the acid in the peat injured the rootlets of some roses, but this can be remedied by neutralizing the peat with a little lime or by using nonacid peat if it is obtainable.

The future of rose breeding depends to a considerable extent on the accumulation of fundamental information on inheritance of rose characters, and on breaking away from many of the established practices. As stated earlier, the accumulation of parentage records is of little value unless it is accompanied by information on numbers of seedlings grown. Undoubtedly some parents will give better progenies than others. This information for some varieties is probably known by some breeders but is not generally distributed. It also seems advisable to start self-pollinations of many present varieties, since they are already so heterozygous that they will probably give rise to something of value. Above all there is a need for systematic investigation by trained workers at institutions well equipped for genetic and breeding work with roses. Such a program would undoubtedly clear up much of the present confusion

SNAPDRAGON

The early history of the cultivated snapdragon (*Antirrhinum majus* L.) is not known. Some records indicate that it was first grown in Italy, whence it spread to the remainder of Europe. At the present time the species is found growing wild in many spots along the Mediterranean coast west of Italy. In one of the earliest published accounts, in 1578, there were described several color variations and two distinctive leaf types, the narrow and the broad. A little later, five varieties, white, purple, blush, yellow, and variable, were known. Soon after this a double-flowered form and one with variegated leaves appeared. At the beginning of the nineteenth century several striped and spotted varieties were listed by various growers. By 1824 a wide range of colors existed from rich orange and yellow to white, with the same types in reds and purples as well as many bicolor forms.

The first-named botanical varieties of *Antirrhinum majus* did not appear until about 1830 or 1835. Among these were *reticulatum*, *youngii*, and *carophylloides*. In 1844 a deep blood-red double-flowered type appeared. The earlier doubles had ranged from white to rose. In the next few decades countless horticultural varieties were introduced each year and were sold as high as $1 per plant. At this time propagation was entirely by cuttings. In 1850, George Parsons, of Brighton, England, introduced a variety that was a distinct change in the arrangement of the colors of the flower. It was white with a deep rose band in the form of an edging to the petals. It was distributed by E. C. Henderson & Sons, in 1852, under the name of Hendersonii.

The snapdragon did not come into its own until the latter half of the nineteenth century. All the earlier varieties had been propagated only by cuttings, and very little had been done with seedlings. The

climate of Scotland and England was very favorable for the production of snapdragons of fine quality, and the flower soon became very popular. The demand for newer and improved varieties stimulated the growing of seedlings, and hundreds of new types were soon developed.

At the present time snapdragons are roughly divided into two groups—(1) florists' varieties and (2) types for outdoor culture. Some varieties, of course, may be placed in both groups. In England and Europe generally, the chief interest is in the outdoor sorts, while in the United States the forcing or greenhouse types are the most important.

The snapdragon flower is so constructed that smaller insects find it very difficult to gain entrance to the nectaries. It requires considerable effort even on the part of a large bumblebee to open the two parts of the corolla. The flower is, nevertheless, frequently visited by large bees, and undoubtedly considerable cross-pollination occurs. Because of this situation, varieties of snapdragons grown for seed should be separated a considerable distance from others. This is especially important for florist varieties, where it is essential that strains be true for type and color.

The practice of growing snapdragons from seed did not become very general until early in the present century. In England and France, seed had been offered by various seedsmen for some time. Most of the old standard varieties, however, were still increased solely by cuttings. In this country, nearly all florists propagated entirely in this manner. As a result many local varieties arose but were not widely distributed. In 1913, snapdragon rust suddenly appeared in the vicinity of Chicago. It had been known in California and along the Pacific coast since 1896. Within a few years after its appearance the disease spread to all sections of this country, to Mexico, and to Canada. The result was almost disastrous to greenhouse snapdragons and practically eliminated propagation by cuttings. The moist conditions and warmth in the cutting bench were also the optimum conditions for snapdragon rust. This situation, and the fact that the disease was not seed borne, stimulated development of better seed-propagated strains. Within a short time a great number had appeared, and today the total list includes many hundreds of varieties.

Most of the present-day varieties have probably arisen from chance crosses made when the commercial seed crop was produced. Even though the seedsman rigidly removes all off-colors and types, the seed produced will usually contain some crosses made by bees. The florist or grower then finds offtype plants the next year. In addition to this source of contamination it is also very probable that some strains usually contain a few hybrids, which carry recessive characters that do not show up until the next year.

Following the widespread distribution of rust, the popularity of the snapdragon began to wane in this country. The florists were able to control the disease under glass, to some extent, by careful attention to watering and maintaining a temperature unfavorable to its development. Plantings outdoors, however, continued to suffer, and the snapdragon began slowly to disappear from parks and home gardens. In California the growing of snapdragon seed was a rather precarious

undertaking. In some years a fair crop might be secured, but on the average the yields were very poor. Many attempts to control the disease by spraying were on the whole unsuccessful.

In 1922 E. B. Mains, then at Purdue University, found two snapdragon plants that showed some resistance to rust. In 1927 he distributed seed to several investigators. Continued selections and self-pollinations in descendants of these strains finally resulted in the development of highly resistant strains of snapdragons. The inheritance of this resistance has been studied by Emsweller and Jones (*117*), White (*545*), and Mains (*327*). In all cases resistance was due to a dominant gene. The inheritance of resistance is shown in figure 22. At the upper left are shown a flower and leaf of a susceptible variety; in the upper right a flower and leaf of a resistant plant; directly between and below, a flower and leaf from the hybrid resulting from a cross between susceptible and resistant. Since resistance is dominant, the first-generation hybrid is completely free from rust. At the bottom are shown flowers and leaves from four of the second-generation plants. Three are resistant and one is susceptible. This count of 3 to 1 is the typical Mendelian ratio when a single pair of contrasting genes is involved. The actual figures from such a cross made in California were as follows: All of the 562 first-generation hybrid plants were completely resistant. One of them was self-pollinated and 550 second-generation plants were grown from the seed. In this large population 405 plants were resistant and 145 were susceptible. A perfect 3:1 ratio would have been 413 resistant to 137 susceptible. The ratio actually secured was off just eight plants. Such a small deviation is not significant, and the ratio secured undoubtedly represents what is called a simple monogenic segregation. Resistance was also found in other *Antirrhinum* species imported from western Europe by the Division of Plant Exploration and Introduction, but these were not used in the breeding of the rust-resistant strains mentioned.

Recently in several localities in California, some of the supposedly resistant plants have again succumbed to rust. Such a situation is not unusual, being common in grain varieties bred for resistance to certain strains of the cereal rusts. It is possible that the condition in California is caused by a new strain or physiological form of the rust organism. Since the rust parasite on the snapdragon is itself a small plant, it is not unusual that it should produce a new strain able to attack otherwise resistant plants. If this should prove to be the situation, the production of rust-resistant strains of snapdragons will be more difficult in those sections where more than one physiological race of rust occurs.

The genetics of the snapdragon has been extensively studied by a large number of workers. The inheritance of color is very complex. According to Miss Wheldale, magenta is in general the most dominant color and yellow the most recessive. By this is meant that magenta is dominant to practically all other colors, while yellow is usually recessive to all others. This explains why seedsmen find that yellow varieties and strains are usually very easy to purify. Since yellow is recessive, plants can exhibit this color only when pure for it. In the same investigations, crimson was dominant to bronze, bronze to

Figure 22.—The way in which rust resistance is inherited in the snapdragon: *A*, Flower and leaf of the susceptible variety; *B*, those of a resistant plant; *C*, resistant hybrid resulting from cross-pollination of *A* and *B*: *D*, *E*, *F*, *G*, flower and leaf from each of four plants descended from the resistant hybrid *C*; this second hybrid generation had a ratio of 3 resistant plants to 1 susceptible.

yellow-tinged bronze, magenta to rose doreé, and rose doreé to ivory-tinged rose doreé. Delilah forms, in which corolla lips are colored and tube is colorless, were recessive to the corresponding nondelilah. For example, crimson was dominant to crimson delilah.

Stock, Double-Flowered

The early history of the stock (*Matthiola incana* (L.) R. Br.) is very obscure. The first authentic records indicate that it was known to the Greeks and Romans and prized by them chiefly as a medicinal herb. By 1542 at least three colors, purple, red, and white, were known, but only in single-flowered types.

The first mention of a double form was in 1568, when a Belgian botanist, Dodvens, described it in a paper dealing with sweet-smelling flowers suitable for chaplets or garlands; and in 1581 an actual illustration appeared. At this time the flower was described as being so double that it was completely sterile. It is not known just when the double form appeared, but it was probably a mutation from the single. From the scant records of the period it seems that the only method of reproducing it was by cuttings. It was not until 1629 that any statement appeared indicating that double-flowered plants could be obtained from seed of singles.

Unfortunately, one of the earliest descriptions of double-flowered stock stated that the doubling was the result of special treatment and frequent transplantation. This belief was held for a long time and many special practices based on superstition developed in the culture of stocks. One of the most interesting descriptions of such practices appeared in a book on gardening in 1675:

Single Flowers Doubled

Remove a plant of stock when it is a little woodded and not too greene, and water it presently; doe this three days after the full, and remove it twice more before the change. Doe this in barren ground, and likewise three days after the new full Moon remove againe, and then remove once more before the change. Then at the third full Moon, viz., eight days after, remove againe, and set it in very rich ground, and this will make it bring forth a double flower; but if your stocks once spindle, then you may not remove them. Also, you must shade your plant with boughs for three or foure dayes after the first removing; and so of Pinks, Roses, Daysies, Featherview, etc., that grow single with long standing. Make Tulipces double in this manner. Some think by cutting them at every full Moone before they beare to make them at length to beare double.

As mentioned earlier, the double-flowered stock plants were propagated by cuttings, but how they came from seed of the singles remained a mystery until it was cleared up by the genetic and cytological research of Saunders (*463*), Frost (*135*), and Philp and Huskins (*408*). For a long time it was generally believed that the double-flowers produced some pollen, which fertilized the singles and formed seed that produced doubles. Directions are still occasionally given for selection of seed from single-flowered plants surrounded by doubled-flowered. An examination of the double flowers, however, discloses no pollen whatever, and it seems certain that if any is ever produced, it is only on exceedingly rare plants.

The differences between a single and a double flower are very striking. The single has four petals, four stamens, and a pistil. When fertilized it produces a long, narrow, flattened fruit containing

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from 30 to 60 seeds. The double flower is composed entirely of petals, which vary from 40 to 70 per flower. There is no trace of stamens or pistil, and, of course, no seed is formed.

The double-flowered plants are desired by both florists and gardeners, and because of this there is active competition among growers of stock seed to produce high double-throwing strains. Accurate counts made by seedsmen have revealed many strains with 80-percent and a few with as high as 90-percent doubles. Usually, however, the proportion secured by florists and home growers is far less. The seedsmen themselves encounter sharp fluctuations; a strain producing as high as 80-percent doubles one year may drop to 50-percent or less the next. As a result of this apparent instability, seedsmen, florists, and gardeners have entertained a belief that doubleness must be controlled by some external environmental factor or factors.

Modern genetic research has now found the fairly simple explanation of this situation. It also points the way to production of reasonably nonfluctuating, double-throwing strains that produce the maximum percentage of doubles. When a large number of single plants are self-pollinated and all seedlings of each one saved, it has been discovered that the singles are of three sorts. Type 1 produces only single-flowered plants, type 2 produces 3 single-flowered plants to 1 double-flowered, and type 3 produces about 54 percent of double-flowered plants and 46 percent of single-flowered. The single-flowered progeny of type-1 singles never produce any doubles in their selfed progenies; they are pure for singleness. The single-flowered progeny of type-2 singles are of two kinds, one-third being pure for singleness and two-thirds like type 2, that is, producing progenies with 3 singles to 1 double. Most of the single-flowered progeny of type-3 singles repeat the performance of their parents, each again producing about 54-percent doubles.[8]

It is now easy to understand how fluctuations in percentage of doubles may occur from generation to generation. Even though a seedsman practices careful plant selection and saves seed only from the high-double strains, he cannot predict with accuracy the ratio of doubles to singles from year to year. It seems highly probable that nearly all stock seed is a mixture of all three types of singles. The percentage of doubles that will develop in any strain, then, is influenced by the number of pure and heterozygous singles that were in the seed field. Since at present there is no certain method of distinguishing the three types of singles except by a progeny test it seems that with ordinary methods of seed production the number of doubles will continue to fluctuate from generation to generation.

The preceding explanation accounts for yearly changes in the proportion of doubles, but it does not explain the occurrence of strains with more than 54 to 57 percent. In fact, it sets such an amount as the maximum proportion that can be secured. How can the strains with over 80 percent of doubles be explained? Miss Saunders has given the explanation. About 20 years ago she noticed for several years the high percentage of doubles developing in a bed of stocks. It occurred to her that some sort of artificial selection could account

[8] It has been shown that occasional pure single plants appear even in type 3 They, of course, bring down the percentage of doubles expected from this type and are an additional source of confusion

for it. A few years later she planted 8 to 10 seeds in each of a large number of pots. When the seedlings were well established, those in each pot were numbered according to their size. When the plants finally bloomed, it was found that most of the large ones were doubles and the small ones singles. In 1923 White (*546*) at the Maryland Agricultural Experiment Station conducted a very similar experiment. He grew a large number of seedlings and then graded them into groups on the basis of size. When the plants bloomed, he too found that most of the large ones were doubles.

S. L. Emsweller has also investigated the problem in genetic studies with stocks. The seedlings were not graded by size, but as soon as the first true leaves were developed, about 150 plants from each of several varieties were transplanted into small pots. All seedlings of a progeny were saved. When the small plants were established, the height, spread, and stem diameter of each were measured each week until the plants began to bloom. They were then classified as doubles and singles, and the mean height, spread, and stem diameter for each group were computed for the weekly intervals. In all cases it was very clear that the double plants were more vigorous than the singles, even in the seedling stage. This does not mean that the smallest double plant was larger than the largest single; there were always a few plants of each type that overlapped It was possible, however, by selecting only the very largest seedlings, to secure 85 to 90 percent of doubles (fig. 23).

Thus the occurrence of unusually high double strains is readily explained. If anyone, florist or gardener, has more seedlings of stocks than are needed, he will invariably discard the weak, small ones and save the largest. On the California flower-seed ranches, stock seed is sown in rows in the field When the seedlings have become well established they are thinned by hand, and naturally the stronger plants are left. This readily explains the frequent occurrence of rows with 80 to 85 percent of doubles. Such rows, of course, came from parent plants that gave the highest possible percentage of doubles.

In the light of these facts, certain recommendations for growing seed of stocks can be made. In the absence of definite information on natural crossing in stocks, it is advisable to self-pollinate all plants selected. A small sample of seed from each selfed plant should be sown in a separate row. Random samples of these seedlings, the first 50 in each row, should be transplanted, the lots again being kept separate. These trial plantings will indicate the genetic type of the parent of each row. Seed from pure singles will give only single-flowered plants; that from simple hybrids, about 3 singles to 1 double; and that from the so-called ever-sporting type, slightly more than 50 percent of doubles. The seed of all pure singles and simple hybrids can then be discarded and a seed crop grown from plants that produced the maximum number of doubles. Such a procedure would require 2 to 3 years but would certainly give high-quality seed. In many sections of California it is possible to maintain such a planting for several years. Emsweller has done so and secured a greatly increased seed yield the second year. It is recognized, of course, that this method would involve extra expense, but it has been profitable with delphinium, hollyhock, and columbine, and it should be with stocks also. If seed

of this type were generally available, and florists and gardeners rigidly discarded all weak seedlings, they should have little trouble in securing stocks running close to 90 percent double. This means that over twice the ordinary amount of seed should be planted, since slightly more than half the seedlings would be discarded in thinning out on the basis of size.

There are several types of stock plants (fig. 24) varying in habit of growth, earliness, and flower color. Unfortunately the importance of

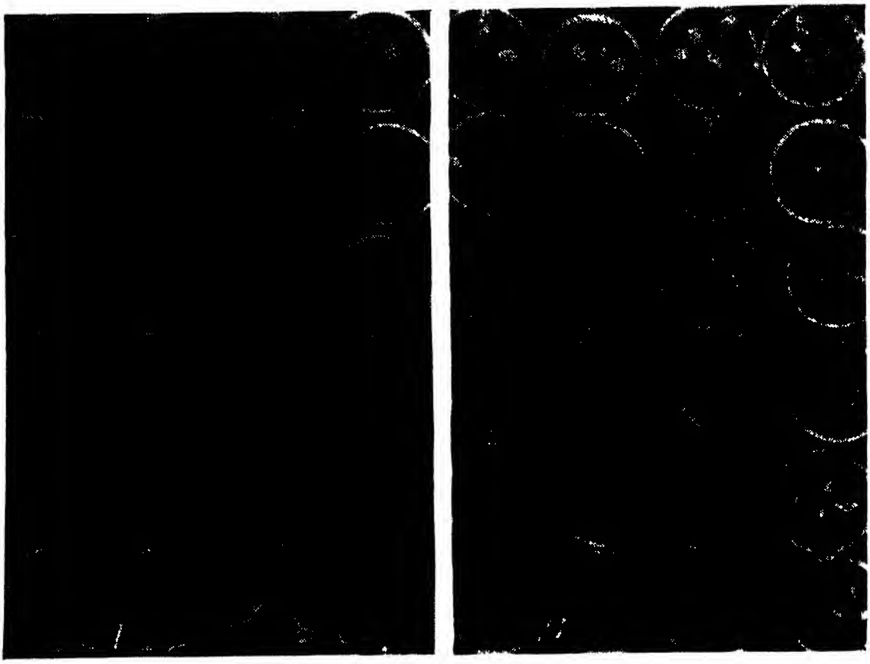

Figure 23.—Stock seedlings selected for size after transplanting: *A*, Group of the extremely large plants, 90 percent of which were double-flowered; *B*, smallest plants, 18 percent of which were double-flowered.

the problem of double flowers has retarded work on inheritance of these characters. Some data are available, however, on inheritance of tall versus dwarf plants and branching versus nonbranching. Tall is dominant to dwarf, and in the second hybrid generation there will be found three tall plants to one dwarf. The situation is not so clear-cut for branching crossed with nonbranching. The first-generation hybrid is branched, and in the second generation there is a close approach to a ratio of 3 branching to 1 nonbranching. These nonbranching plants, however, have some tendency toward branching, which the original nonbranching parent plant did not have.

The future breeding work with stocks will probably be concerned with the inheritance of other important characters. There is also need for the discovery of some simple seedling characteristic to enable florists and gardeners to select with certainty double-flowered plants in the seedling stage.

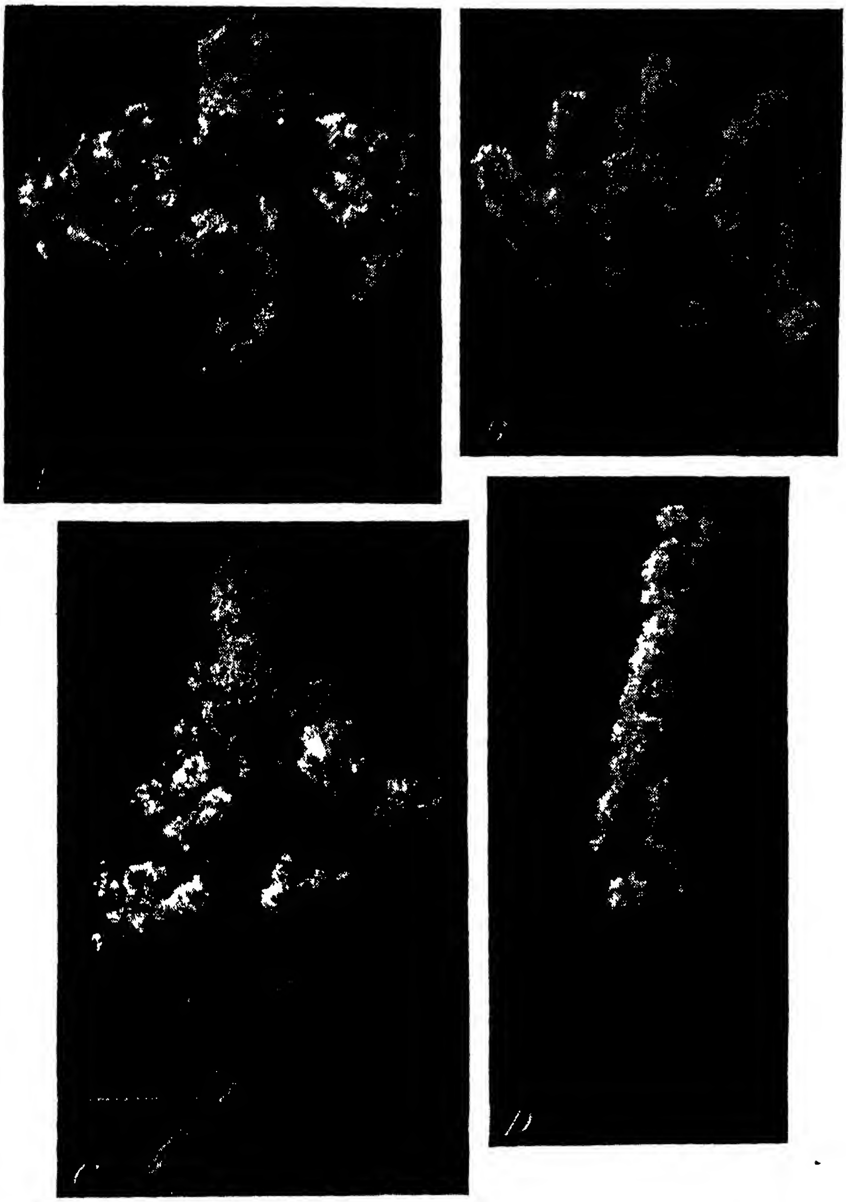

Figure 24.—Four types of double-flowering stock showing variation in growth habit. There are many varieties of each kind including a wide range of colors. (*A*) The tall ten weeks and (*B*) the dwarf ten weeks types are used mostly for bedding, are very early bloomers, and are easy to grow. (*C*) The imperial (branching) and (*D*) the column (nonbranching) types are grown mostly under glass by florists. The column sorts (*D*) are valued for their tall single spike and for adaptability for close planting, thus yielding more salable flower spikes per square foot of greenhouse bench.

Sweet Pea

The sweet pea (*Lathyrus odoratus* L.) was introduced into the Netherlands and England from its native Sicily in 1699. From a figure and description published in 1700 the original type is recognizable as a tall plant reaching a height of 6 or 7 feet, with short flower stems bearing two blooms each. The individual bloom was small and fragrant. The standard was erect, narrowed at the base and cleft at the top. In color the standard was reddish purple, the wings light bluish purple. Figure 25 shows a type closely resembling the wild *Lathyrus odoratus* in comparison with a modern flower.

The evolution of 500 or more distinct garden varieties from this unassuming beginning has been admirably traced by Beal (*40*), and the significance of mutation and hybridization in the process has been interpreted by Babcock and Clausen (*8*). White forms appeared in 1718. In 1731 Painted Lady—pink and white in place of the purple and blue of the original type—was introduced. Scarlet, a brighter self-colored variety presumably derived from Painted Lady, appeared in 1793. Then followed in 1806 a blue variety, in 1817 a striped type, and in 1824 the so-called yellow, more properly primrose. New Large Purple, listed in 1845, implies an improvement in size of bloom. Marked increase in size also occurred in the Countess Spencer variety (1904). The original two flowers per stalk were increased to three with the advent of Invincible Scarlet in 1865 and Crown Princess of Persia in 1868, and they were further increased to four blooms per stalk in the more recent Spencer type. The form of standard was differentiated into three distinct types: grandiflora, erect but larger and broader at the base than the original, appeared in 1888; hooded, with edges inrolled, is an early type; Spencer, with waved standard, is a more recent development. Changes in habit of growth include two recessive dwarf types, the cupid (prostrate) and the bush (erect), and the commercially important winter-flowering type. The winter-flowering sorts are distinguished from other sweet peas by prompt growth and flowering under winter forcing conditions and by lower stature and shorter flower stems. Blanche Ferry, the first of the winter-flowering types, was selected by the wife of a quarryman in northern New York for 25 years before it reached the trade in 1889. Beal has traced the subsequent development of the winter-flowering group from this and subsequent mutations.

All of the changes mentioned thus far are considered in Babcock's analysis to be due to mutation from the original type. The first hybridization in the sweet pea was undertaken about 1880 by Thomas Laxton, of Bedford, England. Thereafter intensive use of crossing served to incorporate the desired colors in the commercial grandiflora, hooded, and Spencer types and to vary the color and form of blooms in the important winter-flowering group. The number of favorable mutations occurring in the sweet pea in two centuries of culture is truly remarkable. These have served as the material from which practical breeders have constructed the varied horticultural varieties of our day.

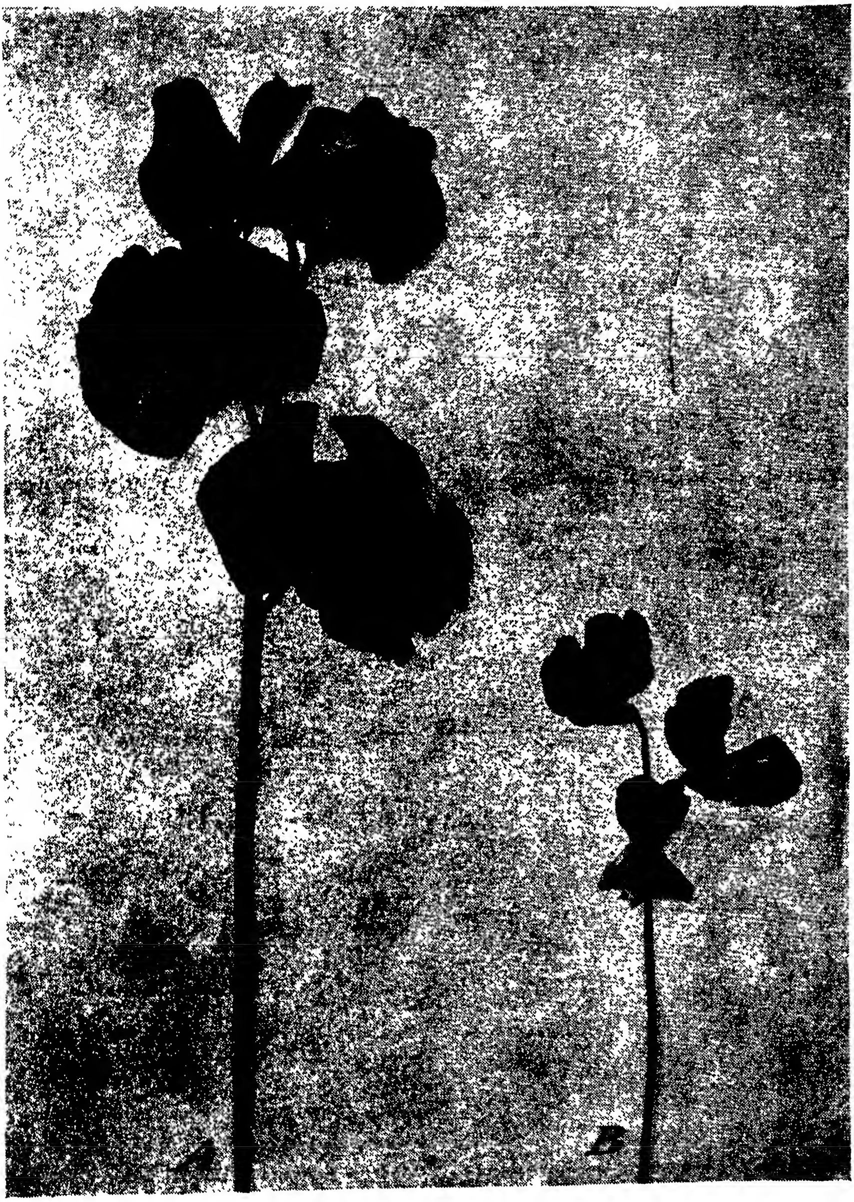

Figure 25.—A modern sweet pea (*A*) and a type closely resembling the wild form (*B*), from which it arose. The greatest part of this development has taken place in the last 25 years.

Hurst (*223*) has presented some examples of the actual procedure followed in producing new combinations by hybridization. W. Cuthbertson produced the Waved King Edward variety as follows.

Parents	King Edward Plain red		Countess Spencer Waved pink	
First generation (F_1)		Plain red		
Second generation (F_2)	Plain red (9)	Plain pink (3)	Waved red (3) ↓ Waved King Edward	Waved pink (1)

The expected proportions of the F_2 population are supplied by Hurst since Cuthbertson did not count the classes. Out of the desired waved red class in F_2, one-third of the plants should be pure breeding and two-thirds segregating again 3 red : 1 pink. Cuthbertson also raised Primrose Spencer by a similar procedure. Hurst also explains the synthesis of Black Knight Cupid in his own experiments:

Parents		Black Knight Tall purple dark-wing				Pink Cupid Cupid red light-wing		
First generation (F_1)				Wild purple Tall purple light-wing				
Second generation (F_2)	Tall purple light- wing (27)	Tall purple dark- wing (9)	Tall red light- wing (9)	Cupid purple light- wing (9)	Tall red dark- wing (3)	Cupid purple dark- wing (3) ↓ Black Knight Cupid	Cupid red light- wing (3)	Cupid red dark- wing (1)

Black Knight Cupid was then "fixed" by saving the progeny of the one-third of this class that were true breeding, and discarding the two-thirds that segregated in the third generation into 3 purple : 1 red. The synthesis of combinations in this manner is simple when the desired genes are available in different varieties and their mode of inheritance is known.

In addition to the many valuable mutations that have made possible the range in color and form of modern sweet pea varieties, other mutations of minor value and actually harmful types have

appeared. Among the mutant forms of minor or novelty interest may be mentioned the "snapdragon" type in which the standard is folded around the wings. This is inherited as a simple recessive to the normal type. Recently Wright has described a variety producing two or even three flower stalks at each node, without loss of size or beauty of the flowers. This may be regarded as a new mutant, evidently of minor commercial value, for no further reference to it has appeared. The change from "long" pollen to "round" is an example of a mutant neither useful nor harmful from the horticultural viewpoint, while "contabescent" anthers, a recessive mutant bearing abortive anthers, and the monstrous "cretin" type with abortive pistil, illustrate harmful mutants. Stone's report of a somatic mutation from recessive cupid to normal tall illustrates that the mutation process is still active in sweet peas.

Although hybridization has been widely employed, natural crossing between varieties of sweet peas is probably infrequent. Until recently there was no authentic record of a successful cross of *Lathyrus odoratus* with any other species of the genus. Barker (*11*) reports success with only one cross between species out of many attempted. This hybrid, *L. odoratus* Kitty Clive × *L. hirsutus* (a weak annual), was fertile; segregation occurred in the second hybrid generation, but the *L. odoratus* type was not recovered. No noteworthy ornamental type appeared in this or later generations. A few seeds were obtained on pollinating the first-generation hybrids from *L. odoratus* × *hirsutus* with pollen from one of the perennial species of *Lathyrus*.

The modern sweet pea leaves little to be desired in form of flower and variety of color. A true yellow is not available though long sought, and brighter shades of present colors are still desired, as well as reds and pinks that do not sunburn. The duplex type, a recent novelty with extra petals producing the effect of added size of bloom, seems worthy of fixing and of hybridizing to extend the range of color and types available. Resistance to diseases, particularly of the root rot group, is needed. A hardier race of sweet peas to endure winter cold and permit fall planting and one enduring summer heat would serve to extend the range of satisfactory garden culture of this excellent annual.

LITERATURE CITED

Literature citations for this article, covering 564 references on flower breeding, are omitted from this volume because of space limitations but are available in the 1937 Yearbook Separate on Improvement of Flowers by Breeding.

APPENDIX

Supplementary Data on Lily Breeding

Classification of the species Lilium

Subgenus *Eulirion:* True lilies. Bulb perennial; leaves linear, lanceolate or lanceolate-ovate.

Section 1. Leucolirion: Trumpet lilies. Flowers trumpet-shaped, horizontal or nodding; perianth segments falcate or spreading at the apex; stamens not divergent.

Examples: *Lilium candidum* L., *L. formosanum* Stapf., *L. longiflorum* Thunb., *L. regale* Wils.

Section 2. Archelirion: Lilies with open, bowl-shaped flowers. Perianth segments widely spreading, broadest below the middle; stamens divergent.

Examples: *L. auratum* Lindl. only, according to Wilson; but also *L. speciosum* Thunb. and *L. tigrinum* Ker according to Baker. Grove adds *L. henryi* Baker and *L. leichtlinii* Hook. f. and comments that the dividing line between Archelirion and Martagon is arbitrary and may need revision.

Section 3. Isolirion: Lilies with erect flowers. Perianth segments falcate, not revolute at apex. Leaves whorled or scattered. Stamens divergent.

Examples: *L. bulbiferum* L., *L. philadelphicum* L., *L. concolor* Salisb.

Section 4. Martagon: Lilies with nodding flowers and strongly revolute perianth parts. Leaves whorled or scattered. Stamens divergent. The Turkscap group.

Examples: *L. martagon* L., *L. chalcedonicum* L., *L. hansoni* Leicht., *L. amabile* Palibin, *L. cernuum* Komarov, *L. superbum* L., *L. willmottiae* Wils.

Subgenus *Cardiocrinum:* Heart-leaved lilies. Bulbs monocarpic (flowering only once); leaves long-petioled, ovate-cordate.

Examples: *L. cordatum* (Thunb.) Koidz., *L. giganteum* Wallich.

List of Lily Hybrids Arranged in Alphabetical Order of the Seed Parents

Species names of the seed parents are followed by the author of the name, the date the name was assigned, the section in which the species is usually placed, and the region to which the species is native. Under the seed-parent headings are listed the pollen parents reported to cross, named hybrids, if any, in quotation marks, and sometimes comment on the results. The practice of indicating a hybrid species by inserting the sign of multiplication (×) before the species name, as *L.* × *testaceum*, has been followed.

Lilium amabile Palibin, 1901. Martagon. Chosen.
× *L. martagon.* Preston reports one success.

L. auratum Lindley, 1862. Archelirion. Japan.
× *L. speciosum* var. *melpomene*="*L.* × *hovcyi.*"
× *L. speciosum* (?)="Mrs. Anthony Waterer."
× *L. speciosum.* Preston reports success.

L. auratum var. *platyphyllum* Baker, 1880. Archelirion. Japan.
× *L. speciosum* var. *magnificum*="*L.* × *parkmanni* var. *haywardi.*"
× *L. speciosum* var. *melpomene* (?)="*L.* × Crimson Queen."
× *L. speciosum.* Stout reports success.

L. auratum var. *rubrovittatum* Duchartre, 1870. Archelirion. Japan.
× *L. auratum.* Stout reports success.

L. bulbiferum L., 1753. Isolirion. Europe.
× *L. croceum* (syn. *L. bulbiferum* subsp. *croceum*). Griffiths reports one worthy hybrid.
× *L.* × *thunbergianum* (syn. *L.* × *elegans*). Berckmüller reports many crosses. According to him the varieties *incomparabile, erectum, grandiflorum, multiflorum,* and Sappho of *L.* × *umbellatum* of commerce are referable to the cross *L. bulbiferum* × *L.* × *thunbergianum.* Berckmüller

further suggests that the name *L. umbellatum* should be restricted to the progeny of this cross and that a new name should be created for those newer varieties of *L.* × *umbellatum* of commerce that are referable to the cross *L. croceum* × *L.* × *thunbergianum.*

L. bulbiferum subsp. *croceum* (Chaix) Baker, 1873. Isolirion. Europe.
× *L. concolor.* Preston reports one success.
× *L. dauricum.* Stout reports success.
× *L. davidi*="*L.* × *crovidi.*" *L.* × *crovidi* × *L.* × *cromottiae*="*L.* × Golden King."
× *L.* × *elegans*="*L.* × Coolhurst hybrid."
× *L.* × *elegans.* Preston and Stout report successes.
× *L. tenuifolium* (syn. *L. pumilum*). Preston reports two natural hybrids.
× *L.* × *thunbergianum* (syn. *L.* × *elegans*). Berckmüller reports many successes and from the resemblance of the progeny to such newer varieties of *L.* × *umbellatum* of commerce as Golden Fleece, Orange King, Invincible, Splendidum, Mahogany, and Vermilion Brilliant, he considers that a new name should be created for this cross, reserving the name *L.* × *umbellatum* for the cross *L. bulbiferum* × *L.* × *thunbergianum.*
× *L. tigrinum*="*L.* × *manglesi.*"
× *L. willmottiae*="*L.* × *cromottiae.*"

L. canadense L., 1753. Martagon. Eastern America.
× *L. grayi.* Stout reports success.
× *L. superbum.* Stout reports success.
× *L. tenuifolium* (syn. *L. pumilum*). Preston reports success.

L. candidum L., 1753. Leucolirion. Europe to Western Asia.
× *L. chalcedonicum.* Griffiths reports promise.
× *L. parryi.* Grove reports success in 1914.
× *L.* × *testaceum.* Preston reports success.
× *L.* × *testaceum.* Griffiths reports success but no hybrids of promise.

L. chalcedonicum L., 1753. Martagon. Greece
× *L. candidum*=*L.* × *testaceum*, natural hybrid (1830?). It is generally agreed that *L. testaceum* is of this origin, but the exact time and place of origin are uncertain. Hybrids closely resembling *L. testaceum* have been reproduced at least three times.

L. concolor Salisbury, 1806. Isolirion. China.
× *L. dauricum*="*L.* × *elegans.*" Berckmuller produced this cross and found the progeny conformed to the description of *L. thunbergianum* Schultes. The latter species is therefore presumably a hybrid and synonymous with *L.* × *elegans.*
× *L. tenuifolium* (syn. *L. pumilum*). One success by Van Fleet, according to Griffiths.

L. dauricum Ker, 1809. Isolirion. Northeastern Asia.
× *L. croceum* (syn. *L. bulbiferum* subsp. *croceum*), Stout reports success.
× *L.* × *elegans.* Stout reports success.
× *L.* × *thunbergianum* (Syn. *L. elegans*). Preston flowered seedlings.
× *L.* × *umbellatum.* Preston flowered seedlings.

L. davidi Duchartre, 1880. Martagon. China.
× *L. pseudotigrinum* (?). Preston reports success.
× *L. tigrinum* var. *fortunei.* Preston reports success. (Probably *L. tigrinum* var. *diploid.*)
× *L. willmottiae* = "*L.* × *davmottiae.*" Preston states that the cross *L. davidi* (the *sutchuenense* form) × *L. willmottiae* was made in 1922. A number of seedlings sent out as "Ottawa hybrids" were later called *davmottiae*, which has resulted in lack of uniformity.

L. × *elegans* Thunberg, 1811. Isolirion hybrid. Japan. Not known wild. Berckmüller has shown that *L. elegans* Thunberg (syn. *L. thunbergianum* Schultes) is a hybrid, *L. concolor* × *L. dauricum.*
× *L. croceum.* Preston and Stout report success.
× *L. dauricum.* Stout reports success.
Preston reports *L.* × *thunbergianum* × *L. dauricum* successful

L. grayi S. Watson, 1879. Martagon. Eastern United States.
× *L. canadense.* Stout reports success.

L. hansoni Leichtl., 1874. Martagon. Northeastern Asia.
× *L.* × *dalhansoni.* Preston reports success.
× *L.* × *marhan.* Preston reports success.

× *L. martagon*. Griffiths reports interesting seedlings.
× *L. martagon album* "*L.* × St. Nicholas." Preston also reports success.
× *L. medeoloides* (?). Stout reports success.
× *L. tenuifolium* (syn. *L. pumilum*). Stout reports 42 pollinations failed, 40 yielded capsules, only 3 seeds germinated.

L. henryi Baker, 1888. Martagon. China.
× *L. auratum*
× *L. candidum*
× *L.* × *princeps* seedling
× *L. regale* — Preston reports success.
× *L. speciosum*
× *L.* × *testaceum*
× *L. tigrinum*
× *L. leucanthum* var. *chloraster* = "*L.* × *kewense*."
× "3 Asiatic Martagons" successful according to Griffiths.
× *L. sutchuenense* (?). Stout reports that plants from bulbs received from C. P. Horsford under this name were self-fertile and fertile with *L. willmottiae* pollen.

L. humboldtii Roezl. and Leichtl., 1871. Martagon. California.
× *L. parryi* { "Frances Larrabee", "Mercer Girl", "Vashon"

L. humboldtii var. *bloomerianum* (Kellogg) Jepson, 1922. Martagon. California.
× *L. humboldti* var. *magnificum*
× *L. parryi* (?)
× *L. roezli*
} Stout reports success.

L. humboldtii var. *magnificum* Purdy, 1897. Martagon. California.
× *L.* × Amos Perry = "*L.* × *gloriosum*."
× *L. humboldti* var. *bloomerianum*
× *L. roezli*
} Stout reports success.
× *L. pardalinum* Kellogg. "Cyrus Gates", "Douglas Ingram", "John McLaughlin", "Kulshan", "Sacajawea", "Shuksan", "Star of Oregon." These are all F_1 seedlings from Griffiths' crosses. Further lines of garden merit were expected from intercrossing and backcrossing these.

L. kelloggii Purdy, 1901. Martagon. California.
× *L. canadense*
× *L. humboldti*
× *L. parryi*
× *L. parvum*
× *L. roezli*
} Feeble fertility is reported by Stout.

L. leichtlinii var. *maximowiczii* (Regel) Baker, 1871. Martagon. Eastern Asia.
× *L. dauricum* var. *venustum* f. *batemanniae* = "*L.* × *horsfordi*." Griffiths also reports a hybrid worth introducing.
× *L. tigrinum*. Preston reports one success.
× *L. willmottiae* = "*L.* × Maxwill."

L. leucanthum Baker, 1901. Leucolirion. China.
× *L.* × George C. Creelman
× *L. regale*
× *L. sargentiae*
} Griffiths reports successful crosses, the first two yielding promising hybrids.

L. leucanthum var. *chloraster* (Baker) Wilson, 1925. Leucolirion. China.
× *L. regale* = "*L.* × *centigale*."
× *L. sulphureum* (syn. *L. myriophyllum* var. *superbum*).

L. longiflorum Thunberg, 1794. Leucolirion. Eastern Asia.
× *L. regale*. Preston reports one success.

L. × *marhan* (*L. martagon* var. *album* × *L. hansoni*). The Netherlands, 1886.
× *L.* × *dalhansoni*
× *L. hansoni*
× *L. martagon* var. *album*
} Preston reports successes.

L. martagon L., 1753. Martagon. Europe and Asia.
× *L. hansoni*. Stout reports success.

L. martagon var. *album* Hort., 1880.
× *L. hansoni* = "*L.* × *marhan*." The varieties "Ellen Willmott" and "E. J. Elwes" were derived from "*L.* × *marhan*."

× *L. bolanderi* S. Wats.
× *L. callosum* Sieb. and Zucc.
× *L. carniolicum* Bernh.
× *L. columbianum* Hanson
× *L. davidi*
× *L. grayi* S. Wats.
× *L. kelloggi* Purdy
× *L. maritimum* Kellogg
× *L. medeoloides* A. Gray
× *L. pardalinum* Kellogg
× *L. willmottiae*
} Grove reports successful crosses but no progeny of note.

L. martagon var. *dalmaticum* Elwes, 1877.
× *L. hansoni* = "*L.* × *dalhansoni.*"
× *L. medeoloides* = "*L.* × *Marmed.*"

L. martagon and varieties.
× *L. hansoni* = "Backhouse hybrids": "Brocade", "Golden Orb", "Mrs. R. O. Backhouse", "Sceptre", "Sutton Court", etc.

L. myriophyllum var. *superbum* (Baker) Wilson, 1925. Leucolirion. Upper Burma. (Syn. *L. sulphureum* Baker 1892.)
× *L. regale* = "*L.* × *sulphurgale.*"
F_2 seedlings are also sold as "*L.* × *sulphurgale.*"
L. × *sulphurgale* × *L.* × *princeps* = "Crow's Hybrid."

L. neilgherrense Wight, 1853. Leucolirion. Southern India.
× *L. wallichianum* = "*L.* × *burnhamense.*"

L. pardalinum Kellogg, 1863. Martagon. California, Oregon.
× *L. humboldti* = "*L.* × *pardaboldti.*" "Dimsdale variety" is a selection from the hybrid.
× *L. washingtonianum* Kellogg
× *L. humboldti*
× *L. parryi*
× *L. maritimum*
} Purdy believes that Luther Burbank's hybrids fall into these four groups, and an additional untraceable group. Many other species crosses were attempted but not kept separated. Some excellent types were produced but L. *burbanki*, which bears the originator's name, is "a nondescript medley"—Purdy.
× *L. columbianum.* Considered promising by Griffiths.
× *L. superbum.* Successful but not promising.—Griffiths.

L. parryi S. Wats., 1878. Leucolirion. California.
× *L. humboldti* var. *magnificum* = "*L.* × Amos Perry."
× *L. pardalinum* = "*L.* × *burbanki.*"
= "Napier's variety."
"*L.* × Frances Fell."
= "*L.* × Peter Puget." Grove states this cross yields fine hybrids, some of which are yellow-flowered.
× *L. parvum* var. *luteum* = "*L.* × *roemeri.*"

L. parvum Kellogg, 1863. Martagon. California, Oregon.
× *L. pardalinum*
× *L. parryi*
} According to Grove these hybrids are attractive but lack "staying power."

L. philadelphicum L., 1762. Isolirion. Eastern North America.
× *L. dauricum* = "*L.* × *phildauricum.*" Skinner discusses his recent crosses in a letter to Preston.

L. pseudotigrinum (?).
× *L. callosum.* Preston reports one success.

L. pumilum DC., 1813. Martagon. Northeastern Asia. (Syn. *L. tenuifolium* Fischer 1812.)
× *L. martagon album* = "*L.* × Golden Gleam." According to Grove, "Golden Gleam" was originally an authentic hybrid but has since been propagated by seed.
× *L.* × *elegans*
× *L. martagon*
× *L. martagon* var. *album*
× *L. regale*
× *L. speciosum*
× *L.* × *testaceum*
} Preston reports successful crosses.

× *L. chalcedonicum*
× *L. monadelphum* Skinner reports successful crosses.
× *L. regale*

L. regale Wilson, 1912. Leucolirion. China.
× *L. tenuifolium.* Claimed by Theodore Albert.
× *L. auratum*
× *L. candidum*
× *L. longiflorum*
× *L. speciosum* var. *rubrum* Preston reports successful crosses.
× *L.* × *sulphurgale*
× *L.* × *testaceum*
× *L. tigrinum*
× *L. sargentiae*
× (*L. sargentiae* × *L. regale* seedling) Stout reports success.
× *L.* × George C. Creelman.
× *L. leucanthum*
× *L. sargentiae* Griffiths reports successful crosses.
× *L. sulphureum*
× *L.* × *sulphurgale*
× *L. browni* Griffiths mentions possible successes.
× *L. longiflorum*

L. roezli Regel, 1870. Martagon. California.
× *L. parryi.* Grove records a fine hybrid of good constitution.
× *L. columbianum*
× *L. humboldti* Stout reports success.
× *L. parryi*

L. sargentiae Wilson, 1912. Leucolirion. China.
× *L. henryi* = "*L.* × *aurelianense.*"
× L. × *aurelianense.* Debras reports seedlings growing, also seedlings of "*L.* × *aurelianense*" selfed.
× *L. regale* = *L.* × *princeps* (syn. "*L.* × *sargale*"). First appeared as a chance seedling. J. W. Crow had some interesting seedlings from the cross *L.* × *princeps* × *L.* × *sulphurgale.*
= "*L.* × George C. Creelman."
= *L.* × Pride of Charlotte. This hybrid is reported to come true from seed. Preston and Stout also report successful crosses.
× *L.* × *aurelianense.* Debras reports success.

L. speciosum Thunberg, 1794. Martagon. Japan.
× *L. auratum.* Preston and Stout report successes.
× *L. candidum*
× *L. henryi*
× *L. regale*
× *L. speciosum* var. *album* Preston reports successful crosses.
× *L.* × *testaceum*
× *L. tigrinum*
× *L. tigrinum* seedling raised by Crow did not reach flowering size.

L. speciosum var. *album* Hort.
× *L. tigrinum.*

L. speciosum var. *magnificum* Hort.
× *L. speciosum* var. *melpomene.* Remarkable hybrid. Griffiths.
× *L. regale*
× *L. tigrinum* Early crosses were successful but seedlings were lost. Preston

L. speciosum var. *rubrum* Hort.
× *L. auratum* = "*L.* × *parkmanni.*"
× *L. tigrinum.* Preston reports early seedlings were lost.

L. superbum L., 1762. Martagon. Eastern North America.
× *L. canadense*
× *L. roezli* Stout reports success.

L. × *testaceum* Lindl., 1845. This hybrid, *L. chalcedonicum* × *candidum*, was first recognized in Germany in 1836 and probably originated in the Netherlands about 1830.
× *L. candidum* = "White Knight." Preston and Stout also report success.
× *L. chalcedonicum* = "*L.* × *beerensi.*" Griffiths reports this cross promising.

L. tigrinum Ker, 1810. Martagon. Eastern Asia.

× *L. elegans* var. *wallacei* (syn. *L. dauricum* var. *wallacei* (Wallace) Wilson). Stout reports success.

× *L. leichtlini* var. *maximowiczi*="*L.* × *tigrimax*." Stout also reports success.

× *L.* × *tigrimax*. Preston reports success. Stout reports success with pollen of the F_1 hybrid *L. tigrinum* × *maximowiczi*.

× *L. sutchuenense*. Stout reports success.

× *L. willmottiae*. Preston has flowered seedlings.

L. tigrinum var. *fortunei* Hort., 1866. Preston describes a form of *L. tigrinum* referred to this variety by Wilson, which is self-fertile. In a recent paper Preston names this form *L. tigrinum* "var. diploid."

× *L. auratum*
× *L. leichtlini* var. *maximowiczi*
} Preston reports success.

L. × *umbellatum* Hort., 1874. Berckmuller considers that this form is a hybrid—*L. bulbiferum* × *L.* × *thunbergianum* (*L.* × *elegans*). The name *L. umbellatum* has been used by Dutch hybridizers for various hybrid lilies of the upright-flowered type.

× *L. bulbiferum*. Griffiths reports one seedling of merit.

× *L.*×*willcrovidi*="*L.* × Fire King."

L. willmottiae Wils., 1913. Martagon. China.

× *L.* × *crovidi*="*L.* × *willcrovidi*."

× *L. dauricum* seedling="*L.* × Grace Marshall"
"*L.* × Lila McCann"
"*L.* × Lilian Cummings"
"*L.* × Phyllis Cox"
} Preston.

× *L.* × *elegans* "Mahogany"="*L.* × *scottiae*."

× *L. davidi*
× *L. grayi*
× *L. speciosum*
× *L. tigrinum* var. *fortunei*
× *L.* × *umbellatum*
} Preston reports successes.

× *L. tigrinum*
× *L. pseudotigrinum*
× (*L. henryi* × *L. sutchuenense*)
} Stout reports successes.

× *L. farreri*
× *L. monadelphum*
× *L. regale*
× *L. washingtonianum*
} Successful crosses reported by Skinner.

Genetic Studies on Ornamental Plants

The utilization of genetic science in practical breeding of flowers is in its infancy. The following brief survey indicates the scope of genetic work on ornamental plants. It will be noted that the characters studied are often of little floricultural interest, and that plants of minor ornamental value have received attention, while many flower favorites have been nearly or wholly ignored. The object of genetic research has been largely to extend knowledge of the operation of the laws of heredity. Ornamental plants have been studied chiefly because they offer easily recognizable characters, and because they are convenient to grow.

The material assembled here is necessarily brief. No claim to completeness is made. Those interested in specific plants will usually find further details in the original publications cited in the bibliography, which appears in the 1937 Yearbook Separate, Improvement of Flowers by Breeding. References are indicated by italic figures following the names of authors in parentheses. Much of the literature up to 1929 is covered by Matsuura (*339*), and up to 1930 by Warner, Sherman, and Colvin (*532*).

Abutilon. (Klebahn, *301*.)

In crosses between *Abutilon striatum* and *A. thompsoni* flower and leaf characters proved hereditary. A range of color shades in F_1 suggested hybridity in the parents. The F_1 proved largely sterile.

Althaea. (Saunders, *458*.)

In a cross of double-flowered × single-flowered the F_1 was intermediate; the F_2 ratio was 1 single: 2 intermediate: 1 double.

Amaranthus caudatus L. (De Vries, *530*.)

The red-leaved type is dominant to the green.

Anagallis arvensis L. (Heribert-Nilsson, *200;* Weiss, *538.*)

Scarlet-flowered × blue produced scarlet flowers in F_1; in F_2 scarlet and blue in no usual Mendelian ratio. Pink (nearly white) × red-flowered yielded red flowers in F_1; in F_2, 3 red : 1 pink-flowered.

Anemone. (Hildebrand, *204;* Rosén, *442, 444.*)

Dark-blue flower color (*Anemone hepatica*) × white (*A. acutiloba*) produced light blue in F_1. Light blue (*A. angulosa*) × dark blue produced an intermediate color in F_1. Blue and red are dominant to white. Red × white often yielded blue in F_1, and in F_2 a ratio of 9 blue : 3 red : 4 white.

Antirrhinum calycinum Lam. (Saunders, *462.*)

Red corolla color is dominant to white, and glabrous stems and capsules to hairy. In the F_1 of red × white corolla, the red color is both diluted and retarded, i. e., the flowers developed in later growth are deeper red than early flowers of the same plant.

Antirrhinum hispanicum Chav. (Baur, *34;* Filzer, *128;* Sirks, *484.*)

In a cross between two self-sterile plants, the F_1 was divisible into two classes, one fertile with either parent, the other with one parent only. Filzer explained Baur's data by assuming three genes for sterility, one of which was common to the two parents.

Antirrhinum majus L. (Bateson, *16;* Baur, *27, 28, 29, 30, 31, 32, 33, 35, 36, 37, 38, 39;* Gairdner and Haldane, *140;* Hackbarth, *160;* Hertwig, *201;* Herzberg-Frankel, *202, 203;* Hiorth, *208;* Kuckuck, *306;* Saulescue, *448;* Scherz, *468;* Schiemann, *469;* Stein, *492, 493;* Stubbe, *499, 500, 501;* De Vries, *529;* Wheldale, *541, 542, 543.*)

Research has given information about some 200 genes in this plant. Color inheritance is complex. Wheldale interprets color expression on the basis of at least seven interacting genes. Baur adds to these a number of basic genes further conditioning, modifying, or intensifying color expression. Baur and his students and others have studied in a large number of mutants the inheritance of form of flower, form of and color distribution in leaves, and stem peculiarities. Most of these mutants, which appeared spontaneously in Baur's cultures, are defective types, and all but one, "crispa" (conditioning wavy leaf margins), are recessive. "Crispa" is dominant, distinctly deleterious in the heterozygous condition, and lethal when homozygous. Mutations have been artificially induced in snapdragon by treatments with radium (Stein), X-rays, ultraviolet light, and temperature shocks (Stubbe). Dwarfs and leaf defects are common; all the induced mutants are inferior types. In general the mutants are similar to spontaneous mutants but appear in higher frequencies. Stubbe records the appearance of some mutants not observed previously, and Stein reports a tendency to gall formation induced by radium. Baur found chemical treatment of stem tips ineffective, and Hiorth obtained no gene mutations from heat-treated pollen grains.

Several instances of linkage have been determined in the snapdragon. Gairdner and Haldane have reported a case of balanced lethals, i. e., two closely linked genes, each causing death of the individual when homozygous, permitting a heterozygous plant to breed nearly true, through elimination of the two homozygous classes.

Antirrhinum species hybrids. (Baur, *34;* Brieger, *55;* Gruber, *156;* Gruber and Kühl, *157.*)

Baur has studied the inheritance of fertility and sterility in several species of *Antirrhinum. A. ibanyezi, A. molle, A. glutinosum, A. hispanicum,* etc., are fully self-sterile; a form of *A. majus* is fully self-fertile. Crosses between self-sterile and self-fertile forms yielded in F_2, 15 self-fertile : 1 self-sterile. Gruber's and Brieger's results indicate that the inheritance of sterility is often more complex. Gruber and Kühl found the radial (peloric) flower character linked with genes for self-sterility.

Aquilegia vulgaris L. (Baur, *30, 32;* Brieger, *54;* Kristofferson, *304.*)

On selfing a dark blue plant, Kristofferson obtained a ratio of 9 dark blue : 3 red : 3 light blues : 1 white. Two genes were assumed, one having additional effects on plant color extension, producing self-color when dominant and white-margined when recessive. Baur found two types of chlorophyll defects—"chlorina" (yellowish green) and "variegata" were each monogenic recessive to the normal green. Chlorina is also a monogenic recessive to variegata. Brieger found flower colors segregating in the pattern of 9 blue : 3 red : 4 white,

with modifying genes controlling intensity of color. Spurless is determined by two polymeric dominants over spurred.

Aquilegia species hybrids. (Anderson and Schafer, *5*, *6*; Blaringhem, *51*; Skalińska *487*.)

Anderson and Schafer found wide petals dominant over narrow and medium length spurs over very long or very short ones in first-generation species hybrids. They observed 16 percent of natural crossing between two strains of *Aquilegia vulgaris*, but none between *A. vulgaris* and *A. skinneri*. Skalińska reports that anthocyanin flower color is linked with straight spurs. *A. californica* × *A. flabellata* yields a fertile F_1 generation and shows both parental types in F_2. The reciprocal cross differs in F_1 and shows no paternal type in F_2. Blaringhem has reported on inheritance in crosses of a mutant type having only female flowers with normal *A. vulgaris*, and also with *A. sibirica* and *A. chrysantha*.

Arabis albida Stev. (Correns, *97*.)

Correns studied three types of periclinal chimaeras in this plant. One type, "leucodermis", is inherited only through the female parent, not through the pollen (maternal inheritance); the other two types are Mendelian recessives.

Argemone. (Correns, *85*; Meunissier, *344*.)

Yellow-flowered *Argemone mexicana* × pale yellow *A. ochroleuca* yielded F_1 plants of intermediate color. *A. mexicana* × *A. platyceras* (white-flowered) produced plants of intermediate type in F_1, and in F_2 a new color type and several new forms in other characters.

Arum maculatum L. (Colgan, *77*.)

Colgan raised 11 seedlings from a plant having black spots on the leaves; of these 5 bore spotted leaves, 6 lacked spots.

Aster tripolium L. (Fleming, *131*.)

Fleming reports that purple flower color is dominant to pink and that pink is dominant to white.

Atropa belladonna L. (Bateson and Saunders, *23*.)

Differences in color of flowers, fruits, and stems, which distinguish the variety *lutea* from the type of the species, showed monogenic inheritance.

Barbarea vulgaris R. Br. (Anderson, *7*; Dahlgren, *105*.)

One type of variegation shows maternal inheritance only. Another type differs from the normal green type by duplicate recessive genes. Somatic segregation also occurs.

Begonia. (Bateson and Sutton, *26*.)

Inheritance of double versus single flowers showed irregularities not fully accounted for.

Bryonia dioica Jacq. (Jones and Rayner, *275*.)

Absence of bloom on the berry proved to be a monogenic dominant to its presence. In a cross between a variety with deeply lobed, rough, dark-green leaves and a variety with less deeply lobed, smoother, and paler leaves, the F_1 was intermediate, and new types appeared in the F_2 population. Number of carpels and number of vascular bundles in the stem were also studied.

Callistephus. (Fleming, *131*.)

From the results of natural crossing it is inferred that purple flower color is dominant to red, and red to white. Deep pink is dominant to white.

Campanula carpatica Jacq. (Pellew, *403*, *404*.)

Blue flower color is a simple dominant to white, but irregular segregation occurs in formation of the pollen grains, so that 97 percent carry the gene for blue, and only 3 percent carry the gene for white. Paler shades of blue are usually recessive to darker shades. White or "patched" seedlings proved recessive to the normal green type.

Campanula medium L. (Correns, *87*; Lathouwers, *309*.)

The "hose-in-hose" or "cup and saucer" type with petaloid calyx proved to be a partial dominant to the normal. In F_2 a ratio of 3 "hose-in-hose": 1 normal appeared. Lathouwers also crossed rose-flowered × white; the F_1 generation was dark violet; in F_2 segregation occurred in the ratio of 9 colored: 7 white, the colored forms falling into the ratio of 9 dark violet: 3 violet: 3 lilac: 1 rose-flowered. This was interpreted on the basis of two complementary genes for formation of anthocyanin and two further genes for color singly conditioning lilac and violet, and together producing dark violet, with rose the double recessive.

Campanula persicifolia L. (Bateson, *18.*)

A dwarf form very distinct from the normal type in appearance proved to be a monogenic recessive to the normal.

Canna. (Honing, *213, 214, 215, 216, 217.*)

Honing studied the behavior of some 18 genes in *Canna glauca, C. indica,* and in segregates from crosses between these species. The inheritance of red leaf margin is complex; in one cross the presence of three complementary genes was indicated, in other crosses monogenic and digenic ratios appeared. A monogenic difference was found responsible for the deep scarlet flower color of *C. indica* as contrasted with yellow flowers of *C. glauca.* Further studies of intensity of flower color, flaking in the flowers, etc., indicated that several genes were involved with ratios disturbed by linkages and lethal genes. Other characters of staminodes, leaves, stems, fruits, seeds were studied.

In crosses of *Canna indica* and *C. aureo-vittata* the proportion of red-margined leaves in the progeny is said to be influenced by differential growth rates of pollen tubes of differing genetic constitution, and also by the constitution of the plasma, so that reciprocal crosses may differ, particularly with respect to the proportions of plants with red-margined leaves. The appearance of a giant type as a somatic mutation is recorded.

Cattleya. (Hurst, *222, 223, 224;* Reychler, *436;* Reychler and Kamerling, *437.*)

In crosses of various Cattleya species, rosy purple flower color proved dominant to white, with two complementary genes involved. Certain albinos therefore produced colored forms on crossing. Other albinos behaved as monogenic recessives to colored. The yellow color of *Cattleya dowiana* var. *aurea* is recessive to the rosy purple color; yellow color in other cattleyas is partially dominant to rosy purple. Reychler mentions a collection of 175 seedlings derived from a cross of two mutants of *C. labiata.*

Celosia cristata L. (Kanna, *282;* Kihara, *300;* Terasawa, *507.*)

"Mosaic" inflorescence (a mixture of red and yellow) yielded on selfing a few reds in addition to the mosaic type. On selfing these reds a ratio of 3 red: 1 mosaic resulted. Kanna also found red dominant to mosaic. In his mosaic lines two types of bud variations were noted. A series of four multiple allels governs flower color (yellow or red) and stem color (green or red). Striping is produced by a recessive gene, which may mutate to the dominant colored condition.

Centaurea cyanus L. (Mekel, *341.*)

A system of three genes is presented to explain inheritance of blue, pink, and white flower color.

Cheiranthus cheiri L. (Blaringhem, *50;* Nelson, *388;* Sirks, *481.*)

The abnormal form *Cheiranthus cheiri* var. *gynanthus*, in which stamens are replaced by extra carpels and petals are much reduced, is a monogenic recessive to normal. In flower color dark red and yellowish brown are independent monogenic dominants to light yellow; dark red is epistatic to yellowish brown. The spontaneous appearance of a female plant with stamens aborted is again recorded by Blaringhem.

Chelidonium majus L. (Dahlgren, *104;* Heijl and Uittien, *196;* Sax, *467;* De Vries, *528, 529, 530.*)

Doubleness is recessive to singleness, but several degrees of doubling appear in F_2. The laciniate leaf type and the "minus" leaf type are independent monogenic recessives to the normal leaf type.

Chrysanthemum. (Miyake and Imai, *362;* Shimotomai, *470;* De Vries, *528.*)

De Vries found yellow flower color dominant to white in *Chrysanthemum roxburghi.* A hybrid, *C. marginatum* (90 chromosomes) × *C. morifolium* (54 chromosomes), is highly fertile and appears to be established as a constant 144-chromosome type; *C. decaisneanum* (74 chromosomes) × *C. indicum* (36 chromosomes) produced a sterile hybrid. A clone with flowers variegated white and magenta, which occasionally produces pure white flowers, is shown to be a chimera.

Clarkia elegans Douglas. (Bateson, *17;* Rasmuson, *432.*)

Four genes for color are recognized; the order of dominance is purplish red, salmon red, light red, and white.

Clarkia pulchella Pursh. (Rasmuson, *432;* De Vries, *528, 530.*)

Three genes for color are recognized; purple is dominant to purplish red; completely colored flowers are dominant to colored with white margins, and colored flowers dominant to white.

Clitoria ternatea L. (Rant, *424*.)

Blue flowers are dominant to white; peloric flowers to nonpeloric.

Coleus. (Correns, *102*.)

A variegated form of *Coleus hybridus*, "albopicta", is influenced by environment, but probably is inherited as a dominant.

Collinsia. (Hiorth, *207*, *209*, *210*, *211*; Rasmuson, *431*.)

Hiorth found white-spotted leaves, red-nerved leaves, and white flowers to be linked in *Collinsia bicolor*. Later he reported a study of 12 genes in this species, which fall into five or more linkage groups. The cross *C. bicolor* × *C. bartsiaefolia* produced a nearly sterile F_1, which was further almost sterile on backcrossing to either parent. Various backcrosses and F_2 and F_3 generations were nevertheless produced. Two partly fertile tetraploids, larger than the diploids, were extracted, one from an F_2 progeny and one from the progeny derived from selfing a backcross plant. Rasmuson reports two complementary genes for flower color in *C. bicolor;* one of these independently produces a red tinge in the stems, which is dilute in heterozygous condition. He also finds that the occurrence of spots on the upper lip of the flower in *C. tinctoria* is a monogenic dominant to the lack of spots. Yellow variegated plants in this species are simple recessives to normal.

Coreopsis tinctoria Nutt. (De Vries, *528*.)

Yellow flowers are dominant to brown (var. *brunnea*).

Cosmos bipinnatus Cav. (Miyake, Imai, and Tabuchi, *363*, *364*.)

A gene for full coloration and a gene for crimson, each acting only in the presence of a basic gene for color production, are postulated to explain the flower color classes crimson, pink, shaded, and white. Basal blotch on the ligulate flowers is considered to be a monogenic dominant to absence of the blotch. The character "double ring" of color on corollas is determined by two complementary genes. The inheritance of pollen color and an abnormal flower type, "bracteoid", have also been studied. Linkage between two genes has been established.

Cypripedium (and *Paphiopedilum*). (Hurst, *220*, *222*, *223*, *224*.)

Rose purple color is conditioned by two complementary genes; hence certain pairs of albinos yield colored offspring on crossing. A third gene produces dilution of color when recessive.

Dahlia variabilis Desf. (Lawrence, *310*, *311*, *312*.)

The dahlia has been shown to be an octoploid, having eight times the haploid number of chromosomes, i. e., a gene or its allelomorph may be represented from one to eight times in a given individual. The yellow and ivory flower colors are both dominant to white, yellow showing tetrasomic inheritance, and ivory, disomic inheritance. Magenta, purple, orange, scarlet, and crimson flower colors are the result of anthocyanin pigments showing over yellow and ivory flavone ground colors. Anthocyanin color apparently shows tetrasomic inheritance. Ivory and yellow flavone colors come from different ancestors, and the chromosomes bearing them do not pair. Similarly the two anthocyanin color genes occur in two different quadrivalent sets of chromosomes. Lawrence has also studied inheritance of a recessive albino flower type which is unstable, producing frequent somatic variation.

Delphinium ajacis L. (Demerec, *110*.)

Demerec studied inheritance of two unstable (mutable) genes, rosa-alpha and lavender-alpha, which frequently revert to their normal allels.

Delphinium orientale Losc. (Beckman, *43*.)

One dwarf type (nana) is a simple monogenic recessive to normal. A second dwarf (nanella) is also recessive, but shows irregular segregation. Double flowers are monogenically recessive to single. The abnormal "ranuncula-flower" type of double is dominant to the common double. Five genes for color are postulated to explain the inheritance of corolla color. The wild color (red-violet) is dominant over all other colors. A case of linkage is reported.

Dendrobium. (Hurst, *223*, *224*.)

Purple flower color is dependent on two complementary genes. Certain albinos yield colored forms on crossing.

Dianthus barbatus L. (Lilienfeld, *324*, *325*.)

In some varieties the flower color may change during the lifetime of the flower. When crossed with normal types this condition was found to be dominant. Singles × doubles give singles in F_1, and a ratio of 3 singles to 1 double in F_2. Normal growth is also a monogenic dominant to dwarf. At present three linkage groups have been established.

Dianthus caryophyllus L. (Batchelor, *15;* Connors, *81;* Saunders, *458.*)

White flowers are dominant to yellow, and red yellow flowers to red. A monogenic difference exists between the bullhead type (extremely double) and the single type; the commercial standard double is the heterozygous form.

Digitalis gloxiniaeflora Hort. (Warren, *534.*)

Nonpeloric is dominant to peloric, purple to white corolla color, and purple spotting on the corolla to brown spotting.

Digitalis purpurea L. (Haase-Bessell, *158, 159;* Keeble, Pellew, and Jones, *290;* Miyake and Imai, *350;* Saunders, *452, 459;* Shull, *475.*)

Conflicting reports exist as to inheritance of some characters. These may be due to differences in the actual varieties studied. White flower color has been reported both as a dominant and as a recessive. Some foxglove plants have the topmost flower of a distinctly different type; which is called peloric. This condition is reported as a simple monogenic recessive to normal. It is also reported as very complex in inheritance.

Digitalis species hybrids. Buxton and Dark, *65;* Buxton and Darlington, *66, 67;* Hill, *205;* Michaelis, *346*)

According to Hill, reciprocal F_1 hybrids of *Digitalis purpurea* and *D. lutea* are unlike, and in each case the hybrid resembles the maternal parent in size of calyx and corolla. Michaelis also found the F_1 progeny from *D. purpurea* (56 chromosomes) × *D. lutea* (96 chromosomes) unlike the reciprocal. The F_1 chromosome number was 76 in the somatic cells. *D. mertonensis* (112 chromosomes), a fertile tetraploid giant, arose from a cross of the two diploid species *D. purpurea* and *D. ambigua* (56 chromosomes in each). It forms only sterile hybrids with other species, both diploid and tetraploid. Various hybrid combinations of diploid species are also sterile.

Dolichos lablab L. (Harland, *194*)

The climbing habit behaves as a monogenic dominant to the bush habit. Flower color, seed-coat color, and plant color are closely correlated. In the F_2 of a cross between two white-flowered varieties, flower color segregated 9 purple: 7 white, and one of the white classes showed intermediate seed and stem coloration. Two genes are assumed: one determines purplish-brown seed coat and purplish hairs on the stipules, the other is epistatic to the first and produces, together with it, purple flowers, black seed, and colored nodes.

Dracocephalum thyrmiflorum L. (Dahlgren, *107.*)

The variety *pallida* (with white flowers, green plants) is a monogenic recessive to the *typica* form (with blue flowers and anthocyanin in the plant).

Epilobium angustifolium L. (Correns, *82, 83*)

The white-flowered variety is a monogenic recessive to the red-flowered type.

Epilobium hirsutum L. (Przyborowski, *413;* Stomps, *495.*)

An abnormal type, "cruciata", is a monogenic recessive to normal. A monogenic difference was found between two types of spines on pollen grains.

Epilobium species hybrids. (Lehmann, *319, 320, 321;* Lehmann and Schwemmle, *322;* Michaelis, *345, 347, 348, 349.*)

Hybrids of most species of *Epilobium* other than *Epilobium parviflorum* and *E. hirsutum* are reciprocally alike, but crosses involving the species mentioned yield reciprocally unlike hybrids. Differences between the reciprocals are found in size of organs, including flower size, in pollen fertility, and in reaction to mildew. The role of cytoplasmic inheritance in these differences has been intensively studied. A giant form twice the normal size but with a diploid complement is described (*322*).

Eschscholtzia mexicana Greene. (Uphof, *525.*)

White flower color is a monogenic dominant to yellow, and white to orange. Orange self-color is dominant to orange base on yellow petals.

Euphorbia pulcherrima Willd. (Robinson and Darrow, *439.*)

The pink form of the poinsettia is a chimeral sport from the red. White is apparently a mutation from red.

Freesia. (Morgan, *376.*)

Several unusual types appearing from spontaneous hybridization are described.

Galeopsis. (Hammarlund, *193;* Müntzing, *380, 381, 382, 383, 384.*)

In *Galeopsis tetrahit,* immunity to mildew (*Erysiphe labiatanum*) is a monogenic recessive to susceptibility; heterozygous forms show partial resistance. Müntzing has studied crossability, cytology, and genetics of species and 80 biotypes. Three groups of species do not intercross: *Ladanum, pubescens-*

speciosa, tetrahit-bifida. Five species hybrids within the subgenus *Ladanum* were produced. A triploid that appeared in the F_2 of a cross *G. pubescens* × *speciosa* gave rise to a tetraploid on crossing with *G. pubescens* as pollen parent. This tetraploid agrees closely with *G. tetrahit* in appearance and in cytological and breeding behavior. Spontaneous *G. tetrahit* is believed to have arisen from the above species in a similar manner. On intercrossing pure lines of *G. tetrahit*, 14 combinations gave high fertility in F_1, and 6 showed partial sterility. Partial sterility is attributed to a lethal gene, which destroys all pollen grains, but only part of the ovules containing it. In *G. tetrahit* and *G. bifida*, inheritance of flower and stem color and rate of sterility have also been analyzed genetically.

Gardenia florida L. (Capinpin, *68*.)

Incomplete data on inheritance of doubleness and fertility were obtained.

Geranium robertianum L. (Dahlgren, *107*.)

White flower color, "leucanthum", is a monogenic recessive to red.

Geum. (Dahlgren, *107;* Marsden-Jones, *333;* Rosén, *443;* Weiss and Rosén, *539*.)

The inheritance of certain characters has been studied in hybrids involving *Geum* species. The presence of anthocyanin is a monogenic dominant to its absence. Large flowers were dominant to small and the F_2 segregation indicated the presence of several genes. Yellow was a monogenic dominant to nonyellow, and red was dominant to nonred. The experimental hybrid *Geum urbanum* × *G. rivale* is indistinguishable from the naturally occurring *G. intermedium;* the reciprocal cross was not successful. Inheritance in *G. intermedium* is often irregular.

Godetia amoena Lilja. (Rasmuson *429, 433*.)

Each of two types of petal spots, on crossing with unspotted *Godetia whitneyi*, proved a monogenic dominant to the unspotted condition. When intercrossed the F_1 showed both types of spot; in F_2, 1 "basal fleck" : 2 double spot : 1 "querfleck" appeared. Rasmuson suggests the two genes are closely linked. Double flowers are dominant to single, but degree of doubleness is influenced by the petal-spot genes mentioned above.

Godetia whitneyi T. Moore. (Rasmuson, *429, 433*.)

Crosses involving different flower colors showed the following monogenic dominants: White over yellow-margined white, red over lilac, rose lilac over lilac, red-spotted over lilac, red over red-spotted, large spot over small spot, and light-margined red over pure red. Single flowers are more or less completely dominant over double ones.

Helichrysum bracteatum Andr. (Dambekalns, *109*.)

Three genes affecting white and yellow involucre color are established. Sulphur and orange are simple dominants to recessive white; the two dominants together condition gold. The third gene, dominant white, inhibits expression of sulphur, orange, and gold.

Hibiscus rosa-sinensis L. (Mendiola, *342, 343*.)

Lobing of seedling leaves was found to be a monogenic dominant to entire leaves. Self-sterility appeared to be correlated with absence of lobing. Single flowers appearing on normally double plants were self-sterile; on crossing with normal singles they bred like doubles. The occurrence of flower color sports is recorded.

Hibiscus sabdariffa L. (Howard and Howard, *218*.)

Eight genes are assumed for color in corolla, calyx, pollen, stem, and leaves. One gene may affect several parts of the plant, e. g., a gene for red in corolla eye, pollen, leaves, and stem is a monogenic dominant to its absence.

Hyacinthus. (De Mol, *372*.)

Hyacinth bulbs X-rayed during flower formation may show somatic variations in flower, leaf, or pollen characters. Somatic variation in flower color on a single flower stalk may be the result of mutations induced by changes in environmental conditions during flower formation.

Impatiens balsamina L. (Bedell, *44;* Hagiwara, *177;* Kanna, *280, 281, 284, 285;* Rasmuson, *425, 432*.)

At least three genes for flower color are known. White is recessive to blue-red, and to blue. A dominant gene for intensification of flower color is also reported. In color patterns, white flecking on colored flowers is reported by one investigator as a simple dominant to nonflecking; another reported it as a recessive. There are two types of double flowers, the common and the "camel lia", which latter is correlated with a dwarfish stature. Single is a monogenic

dominant to common double; but the cross single × camellia gave in F_2, 9 single: 3 common double: 4 camellia double. In a recent study (by Kanna) 16 genes are recognized, 3 lying in each of 2 linkage groups, the others showing largely independent inheritance. Ten genes are concerned with flower color, 3 with flower type. Winged flowers, peloric double flowers, and 3 defective types—"white blotched", "deficient", and "fasciated"—are all simple recessives to normal. A nonheritable type of fasciation also occurs. Striped flowers are determined by a mutable gene.

Ipomoea hederacea Jacq. (*Pharbitis nil*). (Hagiwara, *161, 162, 163, 164, 165, 166, 167, 168, 169, 170, 171, 172, 173, 174, 175, 176, 178, 179, 180, 181, 182, 183, 184, 185, 186, 187, 188, 189;* Imai, *233, 234, 235, 236, 237, 238, 239, 240, 241, 242, 243, 244, 245, 246, 247, 248, 249, 250, 251, 252, 253, 254, 255, 256, 257, 258, 259, 260, 261, 262, 263, 264, 265, 266, 267;* Imai and Kanna, *268, 269;* Imai and Tabuchi, *270, 271, 272;* Miyake and Imai, *351, 354, 358, 359, 360, 361;* Miyazawa, *365, 366, 367, 369, 370, 371;* Sô and Nishimura, *490;* U, *520;* Yamaguchi, *556, 557;* Yasui, *562, 563.*)

In the Japanese morning-glory white flower is a monogenic dominant to colored. At least six different white types exist. Some white × white crosses give colored in F_1, and a 9 : 7 ratio of colored to white in F_2. A complex interaction of complementary genes gives various white types in combination with a variety of different colored tubes, stems, and seeds. Genes modifying color have also been studied. The color of the inside of the tube seems to be controlled by a complex interaction of genes. The inheritance of various types of corollas has been studied, and the action of complementary and inhibiting genes reported. Five abnormal flower types were all monogenic recessives to the normal. Five types of doubleness have also been found to be simple recessives to normal. At least 17 abnormal leaf types are also simple recessives to normal. The literature of *Ipomoea* (*Pharbitis*) is more extensive than that of any other plant discussed here, due to intensive studies of a number of Japanese workers with fundamental objectives. Summary papers now appearing indicate that cultivated forms have arisen mainly through recessive mutations from the prototype; of the 111 genes described, only 15 are dominant; 70 genes have been located in 12 linkage groups (there are 15 pairs of chromosomes); 21 genes are concerned with flower color; 20 genes affect form of the leaf; 10 chlorophyll defects showing genic inheritance and 4 showing plastid inheritance are recognized; 20 genes of low stability (mutable genes) have been described; a provisional map of 1 chromosome showing linkage intensity, and many calculations of crossing over between specific gene pairs have appeared.

Ipomoea imperialis. (Correns, *98.*)

Two chlorophyll deficiencies, "chlorina" (pale green) and "albomarmorata" (white spotted), proved to be independent recessives to normal green.

Ipomoea purpurea (L.) Roth. (Barker, *12;* Imai, *234, 247.*)

Inheritance of flower color is controlled by interaction of several genes. Flaking of petals is a dominant character. Flower color and stem color are intimately related. Flower doubleness was found to be a monogenic dominant over singleness.

Iris. (Bliss, *53:* Colin and Carles, *78;* Reed, *435;* Simonet, *479.*)

Observations on color in bearded iris show Mendelian inheritance of brown-tipped beard, and colored leaf bases. Simonet reports four species-hybrids not yet of flowering size. Colin and Carles find that only species having the same glucosidal reserve can be crossed. Reed has described an F_2 population of a cross between *Iris fulva* and *I. foliosa*, obtained by selfing the garden variety Dorothea K. Williamson, a hybrid between these two species. The F_2 progeny showed a great range of color including types with pure yellow flowers.

Lamium. (Correns, *101;* Müntzing, *378, 385;* Sirks, *482, 485.*)

A peloric flowered form of *Lamium album* was recessive to the normal, but the F_2 ratio indicated five or more genes were involved. Another type with protruding stamens was also recessive, differing from normal by four or more genes. Yellow pollen in *L. hybridum* proved to be a monogenic recessive to red pollen. A type with the lower lips of the flower reduced behaved as a monogenic recessive to normal in *L. maculatum*. A cleistogamous flower type in *L. amplexicaule* showed a simple factor difference from open-flowered, with no dominance. In some species the summer annual habit (surviving only by seed) and the winter annual habit (surviving vegetatively) are modifiable; in *L. purpureum* an obligate winter annual type was found to differ geno-

typically from the facultative winter annual. Inheritance of flower color, time of bloom, height, and vigor were also studied.

Lathyrus odoratus L. (Bateson, *17;* Bateson and Punnett, *20, 21, 22;* Bateson and Saunders, *23;* Bateson, Saunders, and Punnett, *24;* Bateson, Saunders, Punnett, and Hurst, *25;* Gregory, *146;* Punnett, *414, 415, 416, 418, 419, 420;* Stone, *496;* Thoday and Thoday, *508.*

In flower color the following mongenic differences were found, dominant genes being given first: White v. cream, colored v. white, purple v. red, bright v. dull color, full v. dilute color, light v. dark wings, purple v. copper, purple v. maroon. Two identical appearing whites give a purple F_1, and nine purple to seven whites in F_2. A gene for bright color, one for full color, one for light wings, and one for purple act as modifiers for both purples and reds. Other color patterns, as marbling and flaking, are either recessive or heterozygous and not fixable. The four types of growth habit are tall, bush, cupid, and bush-cupid. Cupid × bush gives the normal tall. A form with sterile anthers is a simple recessive to normal. Punnett summarized the data on inheritance in sweet pea in 1924. More recently (1932) he has described five linkage groups and two unassociated genes in *Lathyrus,* corresponding to the seven pairs of chromosomes. Stone reported a somatic mutation from the cupid type to normal tall.

Lilium. (Griffiths, *151;* Heinricher, *198;* Preston, *410.*)

In a cross *Lilium* sp. × *L. croceum,* presence of bulbils was recessive to their absence. In F_2 segregation, parental and hybrid types appeared. In *L. bulbiferum* × *L.* sp. (*tigrinum* ?), bulbils again proved recessive. Griffiths and Preston have listed successful species-crosses.

Linaria. (Correns, *91, 95;* East, *116;* Saunders, *453;* Sirks, *484.*)

Pink flower color in *Linaria* is recessive to blue; orange color in the palate is recessive to its absence. Red × white-flowered *L. moroccana* yielded blue in F_1; in F_2, nine blue: three red: four white. Orange color in the palate is dominant to its absence in *L. vulgaris.* Data on inheritance of sterility collected by Correns have been explained by Sirks according to the scheme applied to *Nicotiana, Veronica,* etc. East reports cross-compatibility of 18 species or varieties of *Linaria.* Purple flowers are dominant to white, and trailing habit to bushy, in *L. cymbalaria.* Copper-colored flecks in the corolla are dominant to nonflecked in *L. broussonnetti* × *perezi.* Four genes are concerned in development of flower color in crosses of *L. sapphirina, L. moroccana,* and *L. reticulata.*

Linum species other than *L. usitatissimum.* (Correns, *99;* Hobusch, *212;* Laibach, *307, 308;* Tammes, *503.*)

In *Linum perenne* and *L. austriacum* the long-styled type is a monogenic recessive; the short-styled type is heterozygous. Self-fertility is apparently dominant to self-sterility. Several grades of self-fertility occur. In *L. austriacum* the difference between long and short style appears to be governed by more than one gene. Tammes has summarized the genetics of *Linum* up to 1928. Hobusch was able to grow the F_1 of *L. austriacum* × *L. perenne* by culturing the normally nonviable seeds on artificial media while still immature. Studies of backcrosses and later generations indicated that the proportion of good seeds is determined by degree of relationship of the parent lines.

Lobelia. (Saunders, *465.*)

An extensive series of flower types from singles through semidoubles to full doubles with five perianth whorls and no stamens occurs in *Lobelia.* Full doubles are sterile, singles are pure-breeding, but genic analysis of semidoubles is not complete.

Lunaria annua L. (Correns, *89.*)

The white-margined leaf type, "albomarginata", is a mongenic recessive to normal.

Lupinus angustifolius L. (Fruwirth, *138;* Hallqvist, *192;* Kajanus, *276;* Roemer, *440, 441;* Sypniewski, *502;* Vestergaard, *526, 527.*)

In flower color, monogenic differences were found between blue and white, blue and red, and red and white. Some crosses between red and white, however, gave a blue F_1, and nine blues : three reds : four whites in F_2.

Lupinus species other than *L. angustifolius.* (Burlingame, *63;* Kajanus, *276; 277.*)

In *Lupinus luteus* the black-seeded type is a monogenic dominant to gray. In *L. mutabilis* blue flowers proved monogenically dominant to white. Work-

ing with *L. apricus* var. *vallicola*, *L. pipersmithi*, and *L. nanus*, Burlingame found a white-striped flower type, which segregated into dark blue, white-striped, and white. This was interpreted on a single gene basis, the white striped being the heterozygous type. Light-blue flowers were mongenically dominant to dark-blue. Dark seeds are associated with dark-blue flowers but probably not determined by the same gene.

Lychnis (including *Melandrium* and *Viscaria*). (Åkerlund, *2;* Bateson and Saunders, *23;* Baur, *30;* Correns, *85;* Shull, *473*, *474*, *476*, *477*, *478;* Tjebbes, *512;* De Vries, *528 530;* Winge, *548*, *549*.)

Lychnis species are normally dioecious, having the male and female flowers on separate plants. Much of the genetic literature concerns the technical problem of sex inheritance. Constant-breeding hermaphrodites are maintained by a system of balanced lethals. Purple flowers are dominant to white. Broad leaf is a monogenic dominant to narrow leaf; it is also apparently sex-linked. Chlorophyll deficient types are recessive to normal green. Winge (*549*) reports that "aurea", a chlorophyll defective, is a sex-linked recessive, restricted to male plants because it is lethal where homozygous. "Variegated", another chlorophyll defect, is limited to female plants. Åkerlund found *Melandrium album* more winter hardy than *M. rubrum*, the F_1 intermediate. Backcrosses to *M. album* were more hardy when the hybrid was the pollen parent than in the reciprocal backcross. Tjebbes recognized four recessive types—"broom growth", "rolled corolla", "transparent corolla", and "biennial type", isolated from inbreeding garden strains of *Viscaria* (*Lychnis*).

Lythrum salicaria L. (Barlow, *13*, *14;* East, *112*, *113*, *114*, *115;* Ubisch, *521*, *523*.)

The styles of this species occur in three different length classes Genetic investigation has been largely concerned with inheritance of style length. A two-factor hypothesis failed to account for certain midstyle types, and a balanced lethal hypothesis at present seems most tenable (East, *115*).

Malope trifida Cav. (Rasmuson, *426*.)

A white-flowered type proved to be a monogenic recessive to red-flowered.

Matthiola incana (L.) R. Br. (Bateson and Saunders, *23*, *24*, *25;* Correns, *83;* Fisher, *130;* Frost, *134*, *135*, *136*, *137;* Goldschmidt, *144;* Kappert, *286*; Lesley and Frost, *323;* Muller, *386;* Philp and Huskins, *408;* Saunders, *451*, *454*, *455*, *456*, *457*, *460*, *461*, *463*, *464;* Snow, *488*, *489;* Tschermak, *518*, *519;* Waddington, *531;* Winge, *550*.)

A cross of rose × white gave a purple F_1 and a trigenic segregation of 27 pale purple : 9 deep purple : 9 rose : 3 deep red : 16 white in F_2. There are also genes that dilute the colors. Two genes are necessary for the production of anthocyanin; if one or both are absent, the flower is uncolored. There is also a gene converting all reds to purple, and another causing the difference between the pure and dull color. Cream is due to pigment in the plastids. It behaves as a monogenic recessive to white. Doubleness is recessive to singleness (for discussion of this question, see section on double-flowering stock). Earliness in blooming is dominant to lateness as is open growth habit to compactness. Saunders has summarized the published data on breeding of stocks to 1928.

Meconopsis cambrica Vig. (Saunders, *458*.)

Doubleness is dominant to singleness, a single gene being involved.

Mimulus. (Brožek, *56*, *57*, *58*, *59*, *60*, *61*, *62*.)

Inheritance of several characters in *Mimulus quinquevulnerus*, *M. tigrinus*, and *M. tigrinoides* has been studied. Distribution of color spots over the entire petal surface behaves as a monogenic dominant to spots limited to half the surface. Single flowers are dominant to doubles, two genes being able to inhibit the double condition entirely or partly. Plants with a terminal flower differing from lower flowers showed dominance of this character. Two genes concerned in flower color have been established in *M. cardinalis*. One determines development of yellow plastids, the other anthocyanin sap color.

Mirabilis jalapa L. (Baur, *28;* Correns, *84*, *85*, *88*, *89*, *90*, *92*, *93*, *94*, *96;* Kanna, *283;* Kiernan and White, *299;* Marryat, *332;* Showalter, *471*, *472*.)

Flower color inheritance in *Mirabilis* shows many cases of intermediate hybrids that cannot be made pure. White × yellow gives pale yellow in F_1 and one white : two pale yellow : one yellow in F_2. White × crimson gives deep magenta, and yellow × crimson, orange red, in a 1:2:1 F_2 ratio in each case. White × crimson, and white × yellow both give magenta rose in F_1, and a very complex F_2. White × white gave white F_1 and F_2. In one instance two whites

gave colored F_1 types. The striped varieties are all heterozygous, segregating to self colors and striped in F_2. In other characters tall is dominant to half dwarf and to dwarf. Half dwarf is dominant to dwarf. Kanna and Showalter independently interpret flower color expression on the basis of two series of multiple allels, one series governing base color, the other modifying color expression. Mutable genes are found in each series. Showalter describes a mutant growth type, "box", which is a monogenic recessive.

Myosotis. (Chittenden, *71.*)

Two genes for flower color are assumed. Pink is dominant to white and blue is dominant to pink.

Nemesia strumosa Benth. (Riley, *438.*)

At least four intrasterile, interfertile lines occur in this self-sterile species.

Nemophila atomaria Fisch. and Mey. (Chittenden, *70.*)

Three genes are postulated to explain inheritance of flower color (lilac, black, red, pale brown) and four other genes for inheritance of color distribution. Apparently lilac is dominant to black, black to red, and red to pale brown. The spotted flower coloration is a monogenic dominant to full-colored.

Nemophila insignis Brand. (Chittenden, *70.*)

Blue flower color is dominant to mauve and to white. Mauve × white produced blue flowers in F_1.

Nemophila liniflora Fisch. and Mey. (Chittenden, *70.*)

At least three genes for flower color and color distribution are assumed. Pale-blue flower color is a simple dominant to purplish blue, and spotted eye (spotted with black) is dominant to full black eye, the two genes showing independent inheritance. One or two basic genes for flower color are also postulated. Black spotted leaves are determined by a single gene, the recessive condition being white spotted leaves.

Nigella damascena L. (Toxopéus, *514.*)

Long stems are dominant to the dwarf form. Crosses between yellow variegated and green plants give green in F_1, and 3 green to 1 yellow variegated in F_2. Single flower was a simple monogenic dominant to normal double. A second double type was dominant to single, and in F_2 no single plants appeared. In studies of color inheritance, colored was dominant to ivory white, blue to violet, and dark blue to pure white.

Nymphaea. (Anonymous, *1.*)

A dominant white is reported.

Odontoglossum. (Hurst, *222.*)

Blotched flower is dominant to self-colored, and yellow-flowered to white.

Orchidaceae. (Colman, *79;* Godfrey, *142.*)

Two lists of successful orchid hybrids, including intergenic hybrids, have appeared.

Oxalis corniculata L. (Nohara, *394.*)

Purple in leaves and in the eye of the flower is monogenically dominant to its absence.

Oxalis rosea Jacq. (Ubisch, *522, 523, 524.*)

Two genes for flower color are recognized, one producing light rose when present in the dominant form, and with a second gene, rose color; white is the recessive. Three genes for style length are assumed; each of the two genes for flower color shows linkage with one of these.

Oxalis valdiviana Hort. (Barlow, *13, 14;* Ubisch, *524.*)

The mechanism of inheritance of style length is, according to Ubisch, similar to that in *Oxalis rosea.*

Paeonia. (Saunders, *449.*)

Twenty-nine hybrid strains have flowered. An F_2 population from the cross *Paeonia albiflora* × *macrophylla* has matured. Two abnormal strains and a few types of ornamental value have appeared.

Papaver rhoeas L. (Becker, *42;* Negodi, *387;* Newton, *389;* Philp, *406, 407;* Rasmuson, *430;* Shull, *476.*)

A white margin of the petals is dominant to its absence. Seven genes for flower color have been isolated and belong in three linkage groups. Nine genes are established by Philp (*407*). Doubleness is determined by several genes. Albinism is a simple recessive to normal, and is independent of flower color. In hybrids of *Papaver rhoeas* and *P. commutatum* the characters of the latter species are largely dominant.

Papaver somniferum L. (De Vries, *528, 530;* Fruwirth, *139;* Hurst, *221;* Ishikara, Kobetsu, and Kojima, *273;* Kajanus, *278, 279;* Kasaeva, *287;* Leake and Prasad, *313, 314;* Miyake and Imai, *353, 355, 356.*)

The basal spot on petals is dominant over its absence. Color in the petal is dominant over white, and purple is dominant over red. When forms are heterozygous for color genes they usually produce progenies with considerable variations in intensity of color. Other color genes have been studied. In plant size, large is a simple dominant over small, and nonstriped petals over striped. Other simple dominants are single over double flowers, and laciniated over entire petals. The cross *Papaver somniferum* × *bracteatum* was successful; the reciprocal produced no viable seeds. The F_1 plants were perennial, very variable, including some monstrous forms. F_2 plants were obtained.

Pelargonium zonale Willd. (Ballard, *9;* Baur, *30;* Moncrieff, *373;* Noack, *392. 393;* Roth, *445.*)

Inheritance of doubleness is incompletely analyzed, singleness is regarded as dominant. A golden-leaved type, "aurea", is a heterozygous form, segregating on selfing into 1 normal green: 2 "aurea": 1 pure yellow. The pure yellow dies in the seedling stage or earlier. The "freak of nature" variety, the leaves of which have white centers and green borders, is not a chimeral type. This leaf character is inherited through both egg and pollen. The chemical nature of dominant rose-pink and recessive salmon-pink flower colors, and of other colors, is interpreted by Moncrieff.

Petunia violacea Lindl. (Ferguson, *126, 127;* Frost, *134;* Harland and Atteck, *195;* Kostoff and Kendall, *302;* Malinowski, *328, 329, 330;* Malinowski and Skalińska, *331;* Matuda, *340;* Moore and Haskins, *375;* Rasmuson, *428;* Sachs-Skalińska, *446, 486;* Saunders, *450, 456;* Savelli, *466;* Terao, *504;* Terao and Nagaharu, *505;* Terao and U, *506;* Tjebbes, *510, 511;* Ubisch, *522;* Westgate, *540;* Yasuda, *559, 560.*)

Color inheritance was mostly simple monogenic with violet dominant over red, also over lilac. Uniform coloring is dominant over green-edged flowers. Violet red × white gave an intermediate F_1, and a 1:2:1 ratio in F_2. Other colors were more complex. Doubleness exists in a wide range of degree. It is caused by stamens becoming petals. Singles × singles give all singles. Singles × doubles give a 1:1 ratio. Doubles × doubles give about 3 doubles to 1 single. In *Petunia axillaris* and *P. violacea,* the progenitors of the cultivated petunias, four pairs of genes determine pollen color. The white flower color of *P. axillaris* was inherited as a recessive in a cross with a royal purple garden form, but the parental purple was not recovered in F_2. Both *P. axillaris* and *P. violacea* are usually self-sterile, and the F_1 is only partly fertile. Garden forms are sometimes fertile, but several grades of self-sterility also occur. Harland and Atteck (*183*) interpret self-sterility on the basis of four multiple allels. By bud pollination they were able to self four normally self-sterile lines, finding one homozygous lethal, one dwarfed, the other two normal in appearance. One or more variegated types show irregular inheritance. Mutations have been induced by X-ray treatment of seed and of flower buds. Some garden petunias are tetraploid, showing irregular behavior on crossing with diploid varieties. Petunia pollen has been shown to stimulate fruit formation in eggplant (*Solanum melongena*), but no seeds are formed.

Phacelia. (Chittenden, *70.*)

Two species, *Phacelia parryi* and *P. whitlavia* were found to cross readily and furnish fertile offspring. Purple flowers proved dominant to bicolored (purple limb and white tube), and bicolored dominant to white. A recessive giant type was found in *P. parryi,* and a recessive entire-leaved form in *P. whitlavia* var. *alba.*

Phlox drummondii Hook. (Flory, *132;* Gilbert, *141;* Kelly, *291, 292, 293, 294, 295, 296, 297;* Kelly and Wahl, *298.*)

Five genes are assumed to account for the inheritance of flower color by Gilbert (*141*). Kelly interprets flower color according to a seven-gene scheme. Cream-yellow is a monogenic recessive to white. A semidouble type is apparently influenced by more than one gene. Salver-shaped corolla is monogenically dominant to funnel-shaped. Entire petals are due to one gene; the recessive form is deeply cut, and the heterozygous form is the "fimbriata" type. Stylelessness and fasciation are each monogenic recessives to normal. Attempts to cross *Phlox paniculata* with *P. drummondii* yielded infertile F_1 progeny; *P. divaricata* × *drummondii* produced an F_1 that developed a few seeds (*132*).

Polemonium. (Correns, *86;* Dahlgren, *104, 106;* Ostenfeld, *399, 400, 401;* De Vries, *528, 530.*)

Blue corolla color in *Polemonium caeruleum* is monogenically dominant to white, pinnate leaf form to bipinnate, normal petal to small narrow petals, and normal green leaves to the pale green (chlorina) type. Both the blue and the white flower colors of *P. caeruleum* proved dominant to the yellow of *P. flavum* in F_1, but these interspecific hybrids were sterile. *P. mexicanum* × *pauciflorum* yielded intermediate forms in F_1, with complex segregation in F_2 and later generations, most of the segregates proving fertile. The reciprocal cross yielded no seed, possibly because *P. pauciflorum* styles are eight times as long as those of *P. mexicanum.* Crosses of *P. caeruleum* with *P. carneum* and with *P. filicinum* yielded only sterile plants in F_1.

Portulaca grandiflora Hook. (Blakeslee, *47;* Blakeslee and Avery, *49;* Enomoto, *118, 119;* Ikeno, *228, 229, 231, 232;* Okura, *398;* Tjebbes, *509;* Yasui, *561.*)

Color of floral parts and vegetative parts are correlated with each other. The interaction of five genes for color has been studied. One special white race is a dominant white with a recessive lethal effect. Pure whites of this type are not produced. When selfed it gives two special whites to one normal white. About one-fourth of the seeds from selfing special white are nonviable. Mosaics on the corolla are heterozygous. A Mendelian analysis has not been made. Doubleness is a simple dominant to singleness. Dwarf type is a simple recessive to normal. This gene reverts to normal fairly frequently. Dwarf plants bear normal branches, and vice versa. Ikeno reported that inheritance of purple-spotted flowers did not conform to Mendelian theory. The species is normally self-fertile, but Tjebbes found a self-sterile variety within which two self-sterile but cross-fertile groups occurred. Okura identified as haploids three dwarf individuals from F_2 and F_3 generations of a cross. These produced an occasional normal diploid on being pollinated with normal pollen.

Potentilla. (Müntzing, *379.*)

Constancy of biotypes within several species of *Potentilla* is due to perfect pseudogamous maternal inheritance. Pollen is not functional, but pollination of emasculated flowers is necessary for setting of seed.

Primula. (Altenburg, *3;* Bateson and Gregory, *19;* Buxton, *64;* Chattaway and Snow, *69;* Chittenden, *70;* Correns, *102;* Dahlgren, *103; 108;* Ernst, *121, 122, 123;* Frimmel, *133;* Gregory, *147, 148, 149;* Gregory, De Winton, and Bateson, *150;* Heinricher, *199;* Huskins, *227;* Keeble and Pellew, *288, 289;* Marsden-Jones and Turrill, *337;* Pellew and Durham, *405;* Raunkiaer, *434;* Sansome, 447; Sömme, *491;* Ubisch, *523;* De Winton, *551, 552, 553, 554;* De Winton and Haldane, *553;* Zollikofer, *564.*)

According to Frimmel (*133*), three pigments occur in flower colors of the garden primrose—anthocyanin, carotin, and anthochlor yellow; 260 color tones are recognizable. Carotin inheritance is monogenic, anthocyanin is digenic, with a factor for red and another for blue, the two together developing a blue-violet; white is recessive. Colors approaching black result from association of the gene for carotin with the two anthocyanin genes. Heterozygotes are expressed as various color tones. Four forms of the "eye" of the flower in *Primula sinensis* are known. Small eye is a monogenic dominant to large eye, and white eye acts in varying degrees as dominant over both small and large eyes. A fourth type, large greenish eye, is a monogenic recessive to normal. Two types of doubleness occur. Each is a monogenic recessive to normal. In several species of *Primula* normal forms have short styles with anthers borne above the stigma, or long styles with anthers at a lower level. These are self-sterile. Crossover types with long styles and anthers at the higher level and short styles with anthers at the lower level are infrequent but self-fertile. The short-style type is a simple dominant to long-style, except in *P. hortensis*, in which two genes are assumed. In *P. obconica* fertility is lower when forms of like style length are crossed than when unlike lengths are crossed. In *P. hortensis* and *P. acaulis* fertilization of normally incompatible forms was accomplished by pollinating stubs after removal of styles. In crosses of *P. juliae* with *P. acaulis* and *P. elatior*, F_2 and backcross data were obtained; short styles were dominant over long, orange over yellow eye. In *P. vulgaris* one recessive gene is responsible for various defects in floral organs. A white-margined leaf type is recessive in *P. malacoides*. In *P. officinalis* a defective type with five extra pistils and no stamens is a simple recessive. Genetic analysis is most advanced in *P. sinensis*, in which 25 pairs of genes and 2 sets of

multiple allels are recognized. Fifteen of these genes have been located in four chromosomes. On selfing *P. kewensis*, a tetraploid species, and several types with respect to style length, fertility, greening in the corolla, and doubleness were obtained, but the parental types were not recovered. Other tetraploid forms which appeared in progenies of diploid *P. sinensis*, proved less fertile than the diploids. Only two of seven genes completely dominant in the diploid, proved completely dominant in the tetraploid, i. e., when one dominant gene and three recessives were opposed. A technical study of linkage in a tetraploid has been made.

Quamoclit. (Nohara, *395.*)

Two flower colors in *Quamoclit pennata* differ by a single gene, without dominance. Stem color may be determined by the same gene. The F_1 of *Q. coccinea* × *Q. pennata* is intermediate and sterile, although *Q. sloteri*, a fixed race, is believed to have arisen from such a cross.

Ranunculus. (Marsden-Jones and Turrill, *334;* Ragionieri, *422.*)

A double, large-flowered form is reported as the result of selection from *Ranunculus asiaticus*. Studies of inheritance of color, sex, and sterility in *R. acris* and *R. bulbosus* have not reached satisfactory analysis.

Reseda odorata L. (Compton, *80.*)

Orange-red pollen color appears to be a monogenic dominant to yellow, and self-compatibility has the same relation to self-incompatibility.

Rhododendron. (Ikeno, *230;* Miyazawa, *368.*)

In studies within the species *Rhododendron indicum* (*Azalea indica*) and in crosses of this species with *R. sinense*, single flowers were monogenically dominant to double, self-colored flowers to variegated, and short stamens to long. The prostrate habit is recessive to upright. Flower size and leaf breadth showed intermediate conditions in F_1. The hose-in-hose type in *R. indicum* var. *kaempferi* was interpreted as a dominant heterozygous form, the pure recessive being the normal type. The apetalous form (petals replaced by stamens) is a similar case but two genes are involved, the apetalous being heterozygous for both, and the normal type double recessive. "Polypetala" (petals separate instead of united) is a dominant heterozygous form, showing a single gene difference from normal.

Rosa. (Erlanson, *120;* Godfrey, *143;* Hurst, *225*, *226.*)

Incompatibility and sterility present serious difficulties in rose breeding. Hurst and Erlanson have shown that extensive polyploid series occur in roses. Hurst found 377 diploids and 629 polyploids in 1,006 species and forms of *Rosa* examined. He considers that five diploid species fundamental to the genus have given rise to many other species in various polyploid combinations. The hybrid tea roses are chiefly tetraploids, and triploid forms also appear among garden hybrids. Pentaploid, hexaploid, and octoploid forms are also found in the genus.

Rudbeckia. (Blakeslee, *48.*)

Two forms with yellow disks were distinguishable by treatment with potassium hydroxide, one turning black, the other yellow. On crossing these two yellow types, purple (normal type) appeared in F_1, and in F_2, 9 purple : 3 "black-yellow" : 4 "red-yellow."

Salvia. (Bateson, Saunders, Punnett, and Hurst, *25;* Blaringhem, *52;* Hrubý, *219.*)

Pink flower color in *Salvia horminum* is a monogenic dominant to white, while violet is the result of interaction of the gene for pink with a second complementary gene which has no effect (i. e., white) when present alone. In the course of six generations of selfing of *S. pratensis* (normally hermaphrodite and blue-flowered), decreased vigor and fertility, and segregation of types with white flowers, female flowers, mosaic leaves, etc., were observed. Attempts to cross *S. nutans* with *S. juriscici* have thus far failed, but selfing of a supposed natural hybrid yielded parental types and an intermediate type like F_1.

Saponaria ocymoides L. (Meunissier, *344.*)

A large, pink-flowered type was found to be dominant to a small white type in F_1.

Saxifraga. (Marsden-Jones and Turrill, *335;* Whyte, *547.*)

Saxifraga potternensis is a tetraploid derivative of the cross *S. rosacea* × *granulata*. Its breeding behavior is uniform.

Senecio vulgaris L. (Trow, *515*, *516*, *517.*)

A scheme of at least 12 genes has been formulated to explain inheritance of a number of differences existing between various named types of this species.

The characters studied include type and color of heads, incision of rays, color of stems, color of leaves, number of nodes. Two or more instances of linkage are recognized.

Silene. (Correns, *91;* Marsden-Jones and Turrill, *336, 338;* De Vries, *528, 530.*)

Pigmented flowers in *Silene armeria* are dominant to white. On crossing white × rose flower color Correns found a monogenic relation, in which white and rose are pure breeding forms and the heterozygote is red. This red type was like the wild form in appearance, but the latter was found to be a pure-breeding red. *S. vulgaris* showed segregation for various characters on selfing. Segregation was noted also in the progeny of a cross of this species with *S. maritima.* A type with defective petals proved to be a simple recessive to normal.

Sisyrinchium angustifolium Mill. (Miyake and Imai, *352, 357.*)

On crossing a self-colored purple with a white with purple eye, a monogenic relation was found, the self-colored proving to be partially dominant.

Tagetes erecta L. (Punnett, *417.*)

The double flower is a monogenic dominant to single, and the flat type of floret to the tubular, the two characters showing independent inheritance. Two or more genes are apparently concerned in the difference between deep orange and lemon-yellow flower color.

Tetragonolobus purpureus Moench. (Nilsson, *391.*)

Yellow flower color is a monogenic recessive to red.

Tropaeolum majus L. (Correns, *98;* Eyster and Burpee, *125;* Rasmuson, *427, 432.*)

Monogenic differences were found between dark-yellow and light-yellow flowers, between red anthocyanin and its absence. Variegated flowers are dominant to self-colored. The climbing type is a monogenic dominant to the dwarf type. Dark-green leaf color is determined by two genes. Two defective types, pale green and white-spotted leaves, each proved to be simple recessives to normal green and showed independent inheritance. Doubleness and fragrance are monogenic recessives. "Super-double" is dominant to both single and common double.

Tropaeolum species hybrids. (Fischer, *129;* Warren, *535.*)

On crossing *Tropaeolum majus* × *T. minus*, red flower proved dominant to yellow, green leaf to variegated, and tall stature to dwarf. The gene for stature was partially linked with that for leaf color. In the hybrid between *T. minus* and *T. peregrinum*, known as *T. pinnatum*, red pigment in corolla and stem proved dominant to its absence, and the relation appeared to be monogenic.

Tulipa. (Hall, *190;* De Mol, *372.*)

So-called "thieves", narrow-petaled forms, are probably mutant forms in tulip varieties. They also occur in tulip bulbs X-rayed during flower formation.

Venidium × *Arctotis.* (Warren, *536, 537.*)

A natural hybrid, *Venedium wyleyi* × *Arctotis stoechadifolia* var. *grandis*, was largely intermediate between the parents but taller and bulkier. In F_2 no clear segregation occurred, but various characters showed dominance of one or the other parental types.

Verbascum blattaria L. (Shull, *473.*)

Bright yellow corolla is a monogenic dominant to pale yellow.

Verbascum phoeniceum L. (Sirks, *480, 483, 484.*)

The inheritance of self-compatibility and self-incompatibility in this species appears to be complex and somewhat irregular.

Verbena. (Eyster, *124.*)

Light variegations in flower color are dominant to heavy variegations; variegation is dominant to dilute self-color; light self-color is dominant to darker self-color.

Veronica gentianoides Vahl. (Correns, *98, 100.*)

The short-styled form is a heterozygous dominant, the long-styled is the homozygous recessive. Style length is further affected by a series of modifying genes. A white-margined form, on crossing with the normal, produced only normal in F_1 and F_2, the defective type showing no genic inheritance.

Veronica longifolia L. (De Vries, *528, 530.*)

The white-flowered type is recessive to the pigmented form, the recessive occasionally appearing as a somatic mutation in large F_1 populations.

Veronica syriaca Roem. and Schult. (Filzer, *128;* Lehmann, *315, 316, 317, 318.*)

Blue flowers are monogenically dominant to rose and white. Self-sterility is determined by a series of multiple allels, which accelerate or inhibit pollen-

tube growth in compatible and incompatible styles. In the F_2 of a cross, four intrasterile but interfertile groups appeared.

Veronica tourneforti C. C. Gmel. (Beatus, *41.*)

In this tetraploid species, number of sepals (four or five) appears to be determined by a series of multiple allels.

Viola arvensis Murray. (Clausen, *72.*)

Study of inheritance of a spot on the style revealed unusual relations, which were explained on the assumption of three or more pairs of genes.

Viola tricolor L. (Clausen, *72, 73, 74;* Kristofferson, *303, 305.*)

The inheritance of flower color is somewhat complex, indicating gene interactions. The presence of a colored spot on the front of the style is dominant to its absence. A second type of spot requires the presence of another gene before it can appear. The prostrate habit of growth in the variety *maritima* is dominant to the erect type of other varieties. Some characters, such as variegations, are apparently non-Mendelian. They appear to depend on plastids in the cytoplasm. The velvety black flower color of *Viola tricolor* var. *nigra* is reported to be determined by three basic genes for expression of color, and five inhibitor genes, which suppress the development of velvety black.

Viola species hybrids. (Clausen, *75.*)

Clausen has reported 25 successful species crosses. *Viola tricolor* and *V. arvensis* cross with many species; *V. cornuta* with only *V. orphanoides* and *V. elegantula; V. calcarata* with only *V. battandieri*. Some new fertile types have been isolated from crosses.

Zantedeschia (*Richardia*). (Ragionieri, *421.*)

In a cross between *Zantedeschia rehmannii* and *Z. elliottiana* most of the characters of the latter proved dominant in F_1, the yellow spathe color being an exception. In F_2 spathe color, size, form, spotting of leaves, etc., showed segregation, but the number in the progenies were too small for interpretation of genic relations.

MISCELLANEOUS FORAGE AND COVER CROP LEGUMES

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THE large family known as Leguminosae, or legumes, contains some of the most interesting and important crop plants. The legumes are distinguished from other plant groups particularly by their flowers and seed pods. The flowers are always irregular in shape, resembling a butterfly, while the pods have two valves or parts into which they readily divide, as in the case of garden beans or peas. Most of the plants with pods that split into halves are legumes. Another distinguishing characteristic of legumes is their ability to take nitrogen directly from the air through association with bacteria that live on their roots, and to manufacture it into food for plant growth. By this means soils are enriched, soil fertility is maintained, and increased crop production is made possible. Some of the minor legumes used solely for cover crops and soil improvement are not so well known as crops grown for forage or grain, but they deserve much wider recognition and could well be used much more extensively.

Improvement work with legumes other than soybeans, alfalfa, and clovers has been very limited, but the importance of this group of plants justifies giving them serious consideration in any improvement program. They have been the subject of some genetic investigation, which will be discussed later.

BREEDING WORK AND POSSIBILITIES

WHILE the legumes considered in this article occupy a place secondary to such crops as alfalfa and red clover, some have proved of great value in sections in which the other legumes do not thrive. The annual lespedezas, for example, because of their ability to grow on soils of low fertility and too acid for alfalfa and clover, have become the chief forage crops from southern Iowa to the Gulf of Mexico. Without them a profitable agriculture in much of that region would be difficult or impossible.

Likewise the vetches and field peas fill an irreplaceable function in the soil-improvement programs of the Southern States, while the cowpea is a standard crop and the bur-clovers furnish winter grazing and soil improvement for millions of acres. Of the more recently introduced crops the crotalarias fill a place on sandy land not otherwise filled, and there are good reasons for believing that some of these species may become leading forage crops in the South.

The present soil-conservation program will require legumes for a variety of situations, but all must have in common the property of

adaptation to reduced fertility and probably to soil acidity. Among these miscellaneous legumes now little known there may be some that with proper attention to selection will prove precisely suited for one or more such situations.

Astragalus

(*Astragalus* spp.)

The genus *Astragalus* contains a very large number of species, commonly called milk vetches. Most of them are especially adapted to dry and arid conditions. None of the species is of much commercial importance, although several are utilized locally and have forage value. No selection or other improvement work has been attempted in this genus, but the drought-resistant quality of the many species would seem to justify the conclusion that for dry-land and arid regions it is perhaps the most likely group from which to expect a legume of agricultural value.

Beggarweed

(*Meibomia* spp.)

The beggarweed or tick trefoil group is composed of a fairly large number of species, few of which have been brought under cultivation. The Florida beggarweed (*Meibomia purpurea* (Mill.) Vail) is the best known and the only one that is grown commercially in the United States. No attempt at improvement has been undertaken, although some natural selection no doubt has taken place, as the crop is harvested from cultivated stands. To what extent improvement is possible no one can say. The species are variable, however, and, no doubt, would respond readily to selection. One botanical variety, *M. paniculata* var. *pubens* (T. and G.) Vail, that has been grown in experimental plantings has growth habits that give promise of usefulness.

WHILE *the legumes considered in this article occupy a place secondary to such crops as alfalfa and red clover, some have proved of great value in sections in which other legumes do not thrive. The annual lespedezas, for example, grow on acid soils of low fertility, and without them a profitable agriculture in large areas from southern Iowa to the Gulf of Mexico would be difficult or impossible. The vetches and field peas likewise fulfill a valuable function in soil-improvement programs. Among the miscellaneous legumes about which comparatively little is now known, many forms especially suited to thrive in difficult situations could undoubtedly be found by intensive study and developed by systematic breeding.*

Bonavist

(*Dolichos lablab* L.)

The bonavist, which in habits, cultural requirements, and uses is much like the cowpea, has been used in Africa and southern Asia from ancient times, and many varieties are known to exist. Nowhere has improvement of the crop been attempted, although improvement with reference to nematode and wilt resistance and other characteristics no doubt could be effected (fig. 1).

Figure 1.—Bonavist (*Dolichos lablab*) showing general habit of growth.

Bur-Clover

(*Medicago* spp.)

Many species of *Medicago* that never are grown as cultivated crops enter into use for pasturage and are recognized as having very great value for this purpose. However, these have received no attention from the plant breeder. Other species that are grown for soil improvement and occasionally used for hay or seed have received some attention by experimenters. In a few instances selections of distinct forms have been made by practical growers who have increased their supply of seed and distributed it locally. Natural selection resulting from regional climatic differences, however, is rèsponsible for much of the improvement in the medicagos.

In the case of spotted bur-clover (*Medicago arabica* (L.) All.) at least two new forms have appeared in the South in recent years. One of these, Manganese bur-clover, was selected and named by A.

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Lee Andrews on his place at Lafayette in eastern Alabama. The other, Early Southern bur-clover, was selected and named by A. F. Ruff at Rock Hill, S. C. Both these varieties are earlier maturing than the commercial spotted bur-clover from which they were selected, and make as good a growth, if not better. A variety of bur-clover grown by H. H. Hopson in Coahoma County, Miss., under the name Giant bur-clover seems to be identical with the Early Southern and probably has the same origin. The Manganese bur-clover is somewhat earlier than the Early Southern and matures about 2 weeks ahead of the

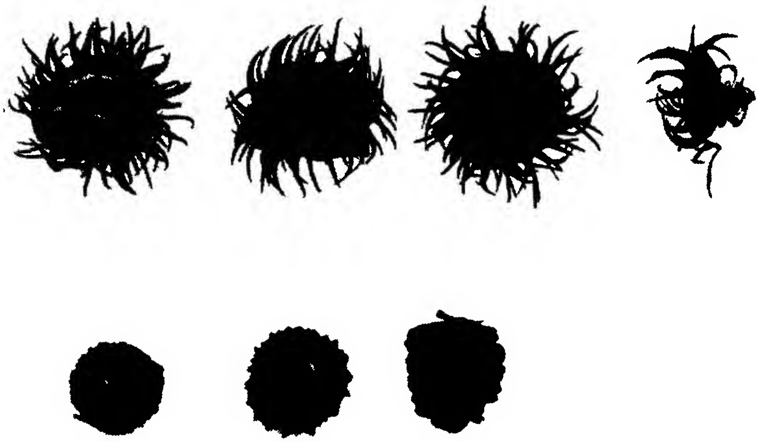

Figure 2.—Coiled seed pods of spiny and spineless forms of spotted bur-clover (*Medicago arabica*). In other species variation in length of spines is not uncommon.

commercial spotted bur-clover. A spineless form of spotted bur-clover has been recognized as a subspecies, but this has never been grown commercially (fig. 2).

California bur-clover (*Medicago hispida* Gaertn.) is very variable and responds to improvement by selection. Where bur-clovers occur spontaneously it is difficult to maintain pure stands of selected forms, and in pastures all that can be hoped for is to increase the relative amount of the improved varieties. Improved selections of bur-clovers were made by the United States Department of Agriculture some years ago and distributed from the United States Plant Introduction Garden at Chico, Calif., but supplies of seed have not been maintained and none are available commercially. The Texas Agricultural Experiment Station has made selections of the California bur-clover and is increasing seed of spineless forms for use in sheep pastures. The many other species are quite variable, like the species just mentioned, and could be readily improved by selection, but so far as is known most of these are in no way superior to the species now used commercially. Thus there seems to be no reason to give them special attention in

preference to the commercial forms. Black medic (*Medicago lupulina* L.) is quite variable and could be improved readily by selection. No work has been reported on the improvement of this plant.

Chickpea

(*Cicer arietinum* L.)

Throughout the western United States attempts have been made to grow the chickpea, which is native to western Asia, but nowhere has commercial production been successfully established. So far as known, no attempt has been made to develop superior varieties adapted to the United States, although it is known that the chickpea is variable and thus presumably could be improved by selection.

Cowpea

(*Vigna sinensis* (Torner) Savi)

A very large number of cowpea varieties are recognized. For the most part these have been developed through several hundred years by natural hybridization and incidental selection rather than by any planned improvement program. Introductions into the United States are recorded in the seventeenth century, but it is within the last century that specific reference is made to named varieties. In the United States in recent years considerable work has been done by experiment stations in the way of bringing existing varieties together for comparative testing. This has resulted in a more extensive use of superior varieties and an elimination of inferior ones. While selection of superior plants has thus been the principal means of improving cowpeas, natural hybridization has played a very important part. Artificial hybridization in recent years has been attempted by a few plant breeders, and at least one outstanding variety has been developed in this way.

A cross between the Groit and Brabham varieties made by workers in the Department of Agriculture resulted in the Victor, characterized by its resistance to wilt and nematodes, which seriously damage most varieties. In the process of continuous growing and natural selection through long periods of time, varieties have changed to suit local conditions with reference to diseases, insects, and climate. Apparently for this reason varieties that have been grown for years in the United States are much more resistant to bean rust than recently introduced varieties, and resistance to wilt and nematode in the Iron, Brabham, Groit, and New Era varieties can be attributed to similar selection. In the case of the Victor, resistance to wilt and nematode has been inherited from its parents, the Brabham and Groit.

The origin of most of the commercial varieties of cowpeas is unknown. The Whippoorwill has been grown under that name since 1840, and the Iron has been known in South Carolina since 1888, but its origin is uncertain, and no information is available as to where the New Era may have come from. From a study of the characters of the Brabham it has been concluded that it is a hybrid between Iron and Whippoorwill, and the Groit is regarded as a hybrid of New Era and Whippoorwill. Improved selections from Brabham and Iron have been made in California and are being grown commercially. Recently a variety of unknown origin was introduced into Florida

and distributed to growers by the State Agricultural Experiment Station, under the name Suwanee. It has given high forage yields and seems to be especially well adapted to Florida conditions.

CROTALARIA

(*Crotalaria* spp.)

Crotalaria, commonly called rattlebox, is one of the newest agricultural crops that has become of commercial importance in the United States within the last 10 years. In India and a few other

Figure 3.—Crotalaria spectabilis, F. C. 18096 (*a*), and the commercial strain from which it was selected (*b*).

tropical regions several species have been in use for a much longer period. Three species are now grown commercially in the United States. These are *Crotalaria spectabilis* Roth, *C. striata* DC., and *C. intermedia* Kotschy. Being variable in plant characters, they lend themselves readily to improvement by selection. Late maturity, which makes the saving of a good seed crop difficult, has been one of the principal objections to crotalaria, and this character was the first in which improvement was attempted. The Department of Agriculture and the North Carolina, South Carolina, Georgia, and Florida Agricultural Experiment Stations working in cooperation have made selections for earliness in all of these species. At Columbia, S. C., an early-maturing variety of *C. spectabilis* has been developed that ripens its seed quite uniformly and 2 weeks or more ahead of the original lot from which it was selected. This is known as F. C. 18096 and in South Carolina has been called locally Carolina crotalaria (fig. 3). Some progress has been made in selecting early varieties

of *C. intermedia* and *C. striata*, but additional improvement is needed before these can be called superior.

Since most of the *Crotalaria* species have been observed only in the wild, it is not possible to say how much improvement may be expected. Up to this time, however, little work has been attempted.

Fenugreek

(*Trigonella foenumgraecum* L.)

Fenugreek (the name means Greek hay) occurs in the Mediterranean region and east as far as India. As grown under cultivation it shows varietal differences that probably are the result of natural regional development rather than artificial selection. So far as known no special improvement work has been done in any country. In the United States fenugreek has succeeded only in California, and there it is grown only occasionally. At the California Agricultural Experiment Station at Davis the continued propagation for years of one of the best introduced strains of fenugreek appears to have resulted in the development of a superior variety well suited to at least that part of the State.

Field Pea

(*Pisum arvense* L.)

The history of the field pea is closely associated with that of the garden pea, since the distinction between the two groups is more one of usage than of botanical characteristics. The more extended use of varieties of field peas, however, has been in comparatively recent times, while the use of the garden pea extends back to earliest history. The development of pea varieties through all these years has been largely the work of the gardener and the commercial seed grower, while the field husbandman has merely grown the varieties apparently best suited to his conditions.

In more recent times a number of experiment stations have made selections from the more promising varieties and introduced them. The experiment stations in Canada and in the United States, particularly in Wisconsin, Colorado, Idaho, and Washington, have been most active in this work. The varieties O. A. C. 121, Wisconsin Perfection, and others represent the results of such work.

The new interest in field pea varieties has been largely in connection with their use as a cover and green-manure crop for the South. The Austrian Winter variety serves well for this purpose, but its susceptibility to disease and its inability to mature a good seed crop under southern conditions has lessened its popularity and called attention to the need for breeding and selection to overcome these difficulties. The Department in cooperation with the Georgia Experiment Station has recently inaugurated a program with such results as the objective. The State experiment stations at Auburn, Ala., and Knoxville, Tenn., have begun similar programs.

By bringing varieties together from every possible source and growing them under southern conditions it is probable that varieties with superior disease resistance and heavy seeding qualities will be found. These can then be used in a breeding program to combine the other desirable qualities needed in a cover and green-manure crop.

Grass Pea

(*Lathyrus sativus* L.)

Lathyrus sativus, commonly known as grass pea, has never become of commercial importance in any part of the United States, although in many places it makes good growth and produces fair seed crops. In India the crop is of some importance, the natives using the seed for food and the plant for forage. A large number of varieties exist, differing in flower and seed color, growth of the plant, and size and shape of the seed. Varieties with large white seeds are superior for human food, while those with strong vegetative growth are preferred for fodder. Varieties of *L. sativus* occurring in India have been studied by Howard and Khan (*11*).[1] While inheritance studies have been carried on with the sweet pea (*L. odoratus* L.), no one has studied *L. sativus* or related species in this way.

Guar

(*Cyamopsis psoraloides* DC.)

Guar, a summer annual, is used in India quite commonly for food for man and beast. Varieties exist, and the plants are more or less variable, but so far as known no special work on improvement has been attempted. In the United States guar has been used in cultural experiments but has not been recognized as having commercial value.

Kidneyvetch

(*Anthyllis vulneraria* L.)

No commercial plantings of kidneyvetch are made in the United States, and so far as known no selection or other improvement work has been attempted in this country. In Wales, selection work with this plant is in progress, but results have not yet been published. In Denmark the improvement of kidneyvetch has been attempted, and strains Tystofte No. 8 and Tystofte No. 28 when compared with commercial kidneyvetch were found to be more productive.

Kudzu-Bean

(*Pueraria thunbergiana* (Sieb. and Zucc.) Benth.)

No work has been done in the improvement of kudzu-bean, but there is no reason to suspect that it would not respond readily to improvement by selection.

Lespedeza

(*Lespedeza* spp.)

The lespedezas or bush clovers as a group are still wild plants. Only one species, *Lespedeza striata* (Thunb.) H. and A., has been long known to agriculture. The others are of such recent introduction that the possibilities of improvement have not been adequately explored.

Agronomically there are two groups of lespedezas. The annual consists of two species, *Lespedeza striata*, or common lespedeza, and *L. stipulacea* Maxim., or Korean lespedeza. The second and much larger group consists of perennial plants, of which one species only, *L. sericea* (Thunb.) Benth., has recently been introduced to agriculture.

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[1] Italic numbers in parentheses refer to Literature Cited, p. 1018.

As is the case with most wild plants, the lespedezas are more or less variable, plants differing in size of leaflets and height of growth, in habit, and especially in date of maturity.

Lespedeza striata, common lespedeza, was first found in Georgia in 1846, spread rapidly over the lower South, and gradually worked north. The character that made this spread possible was undoubtedly the difference in date of maturity between plants. As the species worked farther north the earliest forms seeded and reproduced themselves. This process went on generation after generation, until now the common lespedeza is established as far north as central Indiana.

The variations in habit of growth were made the basis of selection work by the late S. H. Essary, of the Tennessee Agricultural Experiment Station. He began his study of individual plants in 1912 and found a great variation, especially in the habit of growth. Among the variants was one having an erect habit and great productive capacity, which was segregated and put into experimental plantings in 1921. This was introduced by the Tennessee station as Tennessee 76 and is one of the leading late-maturing varieties.

Another variety with larger leaflets and ranker growth than usual was found by J. B. S. Norton, an explorer of the Department of Agriculture, growing wild near the city of Kobe, Japan, and was introduced as Kobe. It is somewhat earlier in maturity than Tennessee 76 but does not grow so erect except in thick stands. Another variety of common lespedeza, inventoried as no. 81742, was collected by Dorsett and Morse, of the Department, in Japan in 1929 and is the earliest maturing form of *Lespedeza striata*. In habit it is nearly as erect as Tennessee 76.

The possibilities for improvement in this species have not been exhausted, but its natural dependence on high temperatures will probably prohibit pushing the species much farther north than its present limits.

The Korean lespedeza also shows variations, especially in date of maturity. Two extra-early forms have been found growing wild in Manchuria. One of these, no. 65280, has been introduced as Harbin; the other, no. 59379, is a week later and makes a little larger growth than Harbin. Neither variety promises much usefulness, because the plant is low in growth habit and the yield is consequently small. They do, however, show the range of possibilities in the development of earliness. Harbin has matured seed at Winnipeg.

Two varieties, an early Korean, no. 19604, maturing about 2 weeks earlier than standard Korean, and a late form, no. 19601, maturing 2 weeks later than the standard Korean, have been selected at the Department nursery at the Arlington Experiment Farm, Arlington, Va. (fig. 4). The early form, no. 19604, has been released for use in northern Iowa, northern Illinois, and adjacent areas. Its habit of growth and yielding ability are like that of standard Korean, and it differs only in earliness. The late form, which is matting in growth habit, is still under observation.

Here again the possibilities of selection have not been fully explored, and in the future better varieties, or varieties better suited to certain conditions, may be selected.

The group to which *Lespedeza sericea*, the perennial lespedeza, belongs consists of several species differing from one another in

botanical characters and in habit of growth. Certain variations in *L. sericea* itself have been noted. The botanical group consists of *L. sericea*, an erect, rather strict plant with narrow leaflets; *L. inschanica* (Maxim.) Schindler, with larger leaflets and lax habit; *L. latissima* Nakai, a prostrate plant; and *L. juncea*, intermediate in habit between *L. sericea* and *L. latissima*. Variations in *L. sericea* are found in width of leaflets, height of growth, coarseness and number

Figure 4.—Korean lespedeza (*Lespedeza stipulacea*). Selected plants showing different growth habits. The plant on the left (*a*), with horizontal lower branches, makes a low matting growth, while *b* is quite upright.

of stems, and earliness (fig. 5). Of the varieties studied, no. 04730 is early, tall, and coarse, no. 12087 is later, with finer stems, and no. 19284 is from a single plant selection out of no. 04730 and is somewhat more uniform than the parent. These variations are neither important nor significant, but they show that a more intensive study may uncover variations of agricultural significance.

One of the most important fields for selection with *Lespedeza sericea* is that of finding forms with a low tannin content. Studies made show that the tannin content varies among individuals, ranging from about 5 or 6 to 10 or 11 percent. From the standpoint of palatability as well as forage value, it is important that a form with low tannin content be found and introduced. Work with this object is being carried on.

The shrubby species, as *Lespedeza bicolor* Turcz. and its allies, have not been studied intensively enough to determine the range of variation, and it does not seem probable at this time that they will offer great possibilities for agricultural usefulness.

Lotus

(*Lotus* spp.)

Several species of *Lotus* (not to be confused with the water-lily of that name) are recognized as being of some commercial importance in several European countries and in Australia, but in the United

States none is recognized as having special value. Seed of *Lotus corniculatus* L. and *L. uliginosus* Schkuhr, two perennial species that are used for hay and pasturage, is available through the seed trade, but no varieties are listed. So far as known no special improvement of these plants has ever been attempted, although varieties with low cyanophoric glucoside content have been reported. The elimination

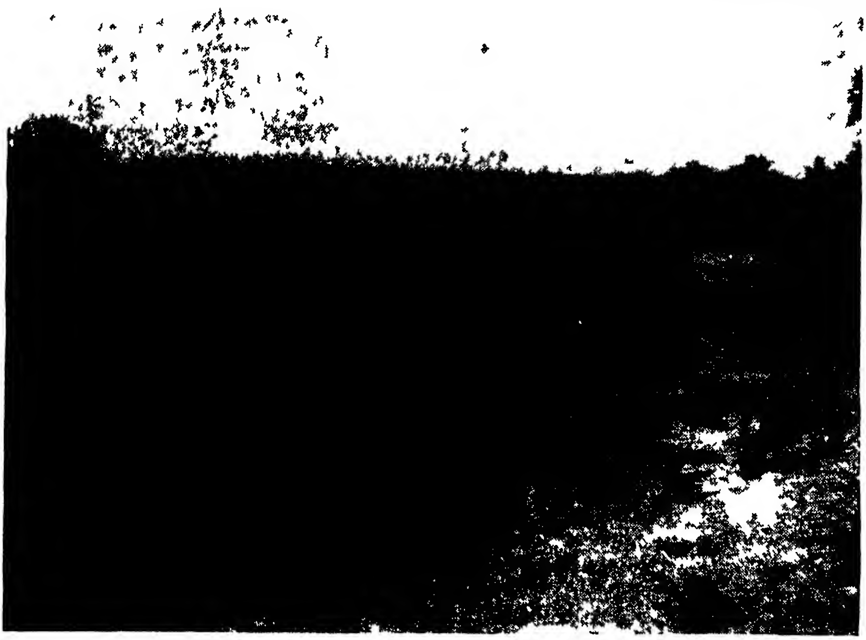

Figure 5.—Lespedeza sericea, showing variation in size and habit of growth. Plants in each row are from seed of a single mother plant

of this glucoside is desirable, since in the course of digestion it is changed to hydrocyanic acid, which is injurious to animals

Lupine

(*Lupinus* spp.)

Several species of *Lupinus* are grown commercially as field crops in European countries, and at least one species is being used in Australia. None, however, has ever been commercialized in the United States, since experimental plantings have indicated that in most places they are not well adapted and cannot be used as economically as legumes now commonly grown.

Varietal improvement in this group of plants has been confined largely to work in European countries, particularly Germany and the Union of Soviet Socialist Republics, where in recent years attempts have been made to produce lupines devoid of alkaloid poisons. Both German and Russian workers report having developed strains with little or no alkaloid, which they call "sweet lupines." The object

has been to produce plants and seed that could be used for both livestock and human consumption without injurious results.

Peanut

(*Arachis hypogaea* L.)

The improvement of the peanut for forage has received little attention. In the United States the experiment stations of Florida and Texas have undertaken hybridization studies, but the results of this work have not yet been published. *Arachis nambyquare* Hoehne and *A. rastiero* A. Cheval. have been used in crossing with the common peanut (*A. hypogaea*), and attempts have been made to introduce other wild species. These offer possibilities but as yet are too little known to justify a statement regarding results.

Pigeonpea

(*Cajanus indicus* Spreng.)

In many tropical countries the pigeonpea is recognized as one of the most valuable legumes. In India a large number of varieties exist and the superior value of some of these is recognized. In the Hawaiian Islands, where the pigeonpea was introduced, improvement of the crop has been undertaken and selection and breeding work have resulted in the production of superior varieties. New Era strain X is recognized in Hawaii as one of the most desirable and much superior to the strains from which it was produced. In the United States varieties have been grown for selection work at several southern stations. The plantings at the Florida Agricultural Experiment Station at Gainesville have been the most extensive. Wide variation in the plants has been observed and early-maturing varieties have been selected, but no variety has been found sufficiently well adapted to justify commercial use. One variety has matured as far north as Washington, D. C., but seed production has been light.

Sainfoin

(*Onobrychis vulgaris* Hill.)

Sainfoin has been grown in France and other European countries for over 300 years. In the United States it has never become of commercial importance, although in experimental trials at a number of experiment stations it has made good growth. A number of botanical varieties are known to exist, but improvement of most of these for agricultural use so far as known has never been attempted. Commercial sainfoin is quite variable and includes both biennial and perennial forms. Improvement by selection in both of these no doubt could be easily effected. The Washington Agricultural Experiment Station at Pullman is making selections of sainfoin with the idea of obtaining better adapted varieties.

Serradella

(*Ornithopus sativus* Brot.)

In central Europe serradella is used on acid sandy soils, but in the United States production or use on a commercial scale has never been successful. Improvement of varieties is reported from Germany, although the amount of work seems to have been very limited.

Sesbania

(*Sesbania macrocarpa* Muhl.)

The seed of sesbania as found in the commercial trade is gathered from wild and volunteer plants and represents the species as it is found growing naturally. The plant grows in wet or moist soils in the Southern States. No attempts at improvement have been made.

Sulla

(*Hedysarum coronarium* L.)

Attempts to grow sulla in the United States have indicated that while it succeeds fairly well in a number of places so far as growth is concerned, it does not appear to have a place in competition with legumes now commonly grown. In several European countries it is grown as a commercial crop and is considered as having superior value for special localities. While varieties are known to exist, few attempts at varietal improvement seem ever to have been undertaken. In New South Wales a special strain was selected for many years and tested on the experimental farms, but for other countries no work is reported.

Velvetbean

(*Stizolobium* spp.)

The Florida velvetbean (*Stizolobium deeringianum* Bort) is one of the leading legume crops in the southeastern United States. It was introduced in Florida previous to 1875 and for many years was confined largely to that State, since it would seldom mature much farther north. Attempts to grow the crop in Georgia and Alabama later resulted in the selection of mutants that required a much shorter season to mature and were well adapted otherwise. In 1906 Clyde Chapman, of Sumner, Ga., observed an early-maturing plant that he selected and grew under the name Hundred Day Speckled. This variety later became known as Georgia and is the earliest maturing commercial variety now grown.

In 1908 R. W. Miller, of Broxton, Ga., selected an early-maturing variety that was grown as Clark's velvetbean, but this proved to be so like the selection made by Chapman that it later was considered identical with the Georgia.

In 1911 a Mr. Blount, of Flomaton, Ala., selected an early-maturing variety, which he called Alabama. This was not quite so early maturing as the Georgia but was sufficiently good to become commercialized and is still being grown.

A variety of velvetbean known as the bush velvetbean (fig. 6) was selected on the farm of Roan Beaseley at Kite, Ga., about 1914. As its name implies, it is a bush or bunch variety, lacking the twining habit of other velvetbean varieties. In work with this variety at the Mississippi branch experiment station at McNeill, H. R. Reed noted a white-seeded variant and made selections of it with the idea of using the white seed character to identify the bush variety. This selection did not prove to be stable as to seed color, and subsequent selection was continued. Now after 10 years a variety seems to have been obtained that reproduces true to color.

At the Florida station a hybrid variety known as Osceola was produced by John Belling, who made a cross between the Florida velvetbean (*Stizolobium deeringianum*) and the Lyon velvetbean (*S. niveum* (Roxb.) Kuntze). This is a vigorous, heavy-yielding variety with a medium season, so that it is adapted as far north as central Georgia.

Figure 6.—Bush velvetbean

The velvetbean offers opportunity for much further improvement, and the importance of the crop suggests that such work could be done with profit.

Vetch

(*Vicia* spp.)

A large number of species of *Vicia* are in general use, all of which go under the general name vetch. The species that are of importance commercially are *Vicia villosa* Roth, *V. sativa* L., and *V. pannonica* Crantz. Others that are occasionally used are *V. atropurpurea* Desf., *V. calcarata* Desf., *V. monantha* Desf., *V. dasycarpa* Ten., and *V. angustifolia* Grufberg. So far as known, vetches are close-pollinated, and seldom, if ever, does crossing take place. All species seem to be variable, but differ somewhat in this respect. Hairy vetch (*V. villosa*) is much more uniform than common vetch (*V. sativa*), and while several species seem to be less variable than hairy vetch, none are so uniform but that improvement can be made by selection.

Common vetch has been grown in the Mediterranean region for centuries, and through regional selection and otherwise a large number of varieties have been developed, differing in seed color and growth

characteristics. Much of the improvement in this crop, no doubt, traces to selections made by local growers, but natural selection due to continued regional production probably also played a part. In later years experiment stations have developed improved varieties for local use, but published statements regarding such work are very meager.

Most of the work in vetch improvement in the United States has been carried on at Corvallis, Oreg., by cooperation between the Department and the Oregon station.

In this region common vetch has been grown for many years, and the commercial strain now grown is the result of natural selection through this long period. The winter temperatures of western Oregon and western Washington represent about the extreme of cold that the most hardy strain of common vetch will endure. Thus the variety that has survived and been developed and increased here in commercial production represents one of the most winter-hardy of the common vetches.

Since other vetches are of very recent introduction commercially, natural selection has played little if any part in the development of varieties.

In the case of both hairy vetch and common vetch the work of the Oregon station, cooperating with the Department, has resulted in improved varieties that already have been or are becoming commercialized. Here a vigorous growing variety of smooth vetch (*V. villosa* var.), lacking the heavy pubescence of hairy vetch, was selected in 1926 by H. A. Schoth and is now grown quite extensively. A good deal of the seed of *V. villosa* imported from central Europe under the name hairy vetch is smooth vetch and resembles the smooth vetch variety grown in Oregon. Of the common vetch (*V. sativa*) selections that have been developed, a white-flowered variety, F. C. 02830, that is somewhat superior in vigor and winter hardiness to commercial Oregon common vetch and was selected by Schoth in 1915, is perhaps outstanding. The white-flower character offers a ready means of identification in the field and will enable the grower to keep his seed pure.

In the Netherlands, Denmark, and other European countries where common vetch is grown, improved varieties adapted to local conditions have been developed, but none of these, so far as they have been tested in the United States, has proved superior to varieties developed in this country.

GENETIC STUDIES IN MISCELLANEOUS LEGUMES[2]

Inheritance studies have been made in few of the so-called miscellaneous forage legumes. From general observation and in some cases from definite experimental demonstrations it is known that a number of legumes are self-pollinated and rarely if ever are cross-fertilized. Whether or not these can be crossed or hybridized has in many cases not been determined.

Studies of several species of *Phaseolus* in India indicate that the urd bean (*P. mungo* L.) and the mung bean (*P. aureus* Roxb.) are

[2] This section is written primarily for students or others professionally interested in breeding or genetics.

usually self-pollinated, although the mode of anthesis in many cases would permit of cross-pollination.

Unpublished observation of legume plantings in the United States indicates that *Crotalaria, Vicia, Lathyrus,* and the annual species of *Medicago* are largely self-pollinated and seldom if ever cross-fertilize. A close study of anthesis in such cases, however, might indicate a means of effecting crossing.

No work on crossing lespedezas has been done. The technical difficulties are of the same order as those presented by the clovers and are due to the fact that the flowers are small and difficult to manipulate. There is another difficulty in addition. The three commonly known species of *Lespedeza*—*L. striata* (Thunb.) H. and A., *L. stipulacea* Maxim., and *L. sericea* (Thunb.) Benth.—have flowers of two kinds, and both kinds occur in the same cluster. One set of flowers bears a corolla and is therefore conspicuous; the other and more numerous kind has closed flowers with reproductive parts complete but with no corolla. These flowers are consequently self-fertile. Although definite data are wanting, the conclusion drawn from observation is that these species are self-fertile. No sign of hybridizing has been observed, though the species have been grown side by side for years. The progeny from the seed of individual plants is always true to the mother plant.

In the case of serradella, which has been reported as self-fertile, plants inbred for four generations did not lose vigor.

While crossing in many legumes seems to be uncommon, there are others that cross readily and are naturally cross-fertilized. Species that have been used in inheritance studies are the cowpea (*Vigna sinensis* (Torner) Savi), chickpea (*Cicer arietinum* L.), adzuki bean (*Phaseolus angularis* (Willd.) Wight), bonavist (*Dolichos lablab* L.), horsebean (*Vicia faba* L.), pigeonpea (*Cajanus indicus* Spreng.), lupine (*Lupinus* spp.), peanut (*Arachis hypogaea* L.), velvetbean (*Stizolobium deeringianum* Bort), and field pea (*Pisum arvense* L.).

Chickpea

(*Cicer arietinum* L.)

While self-pollination is the general rule in *Cicer arietinum*, varietal crosses have been recorded. In 1915 Howard, Howard, and Khan (*10*) reported the growing of selections that split in the F_2 generation, indicating natural crossing. Their observations were not made in sufficient detail, however, for the deduction of the various color factors present.

More recently inheritance studies were made by Khan and Akhtar (*13*) relating to color and number of flowers. In making artificial hybrids it was found that in order to prevent accidental crossing emasculation should be effected the evening of the second day preceding fertilization. The flowers open naturally on bright days between 9 and 10 a. m., and the pollen should be applied at this time. Five crosses were studied and the following results reported (*13, p. 155*):

(1) The flower color depends upon the interaction of several factors.
(2) Blue color depends on a single factor *B*.
(3) Pink color is produced by a factor *P* in the presence of *B*.

(4) In the absence of *B* the flower is white whether *P* is present or absent.
(5) Greenness in the standard is developed in the absence of the factor *W*. Greenness is therefore recessive to nongreen.
(6) Singleness depends upon a factor *S* and is dominant to doubleness.

Cowpea

(*Vigna sinensis* (Torner) Savi)

The cowpea has been recognized as one of the legumes that offer excellent facilities for inheritance studies, and investigations by Spillman and Sando, and in particular by S. C. Harland, have indicated what may be expected by more extended research. In studies made by Spillman and Sando (*16*) flower color was found to be correlated with coloration in the seed coat, joints, peduncles, stipules, and petioles, and complete linkage was observed in certain seed-coat-color factors.

It was determined that the presence of anthocyanin coloration in the stem and leafstalk is due to a single unit factor, dominant to its absence.

In the case of certain seed-coat-color patterns, two factors that are inherited independently were found to influence the color pattern, resulting in the expected 9:3::3:1 ratio.

Seventeen Mendelizing factors of cowpeas were definitely identified. These factors with the characteristic effect they produce are as follows:

A. Seed pod curved after the manner of the alfalfa seed pod.
B. Brown seed coat.
D. Dense speckling, characteristic of the New Era variety.
E. Narrow eye.
F. Very fine and dense speckling, giving rise to blue seed coat.
G. Dotting; converts Holstein spots into numerous small ones.
H. Holstein type of seed-coat spotting.
I. Eye with indefinite margin.
L. Longitudinal furrowing of the surface of the seed.
N. Presence of anthocyanin pigment factor.
P. Purple seed coat.
R. Red seed coat. (This is the general factor for color, the absence of which determines white seed coat, white flowers, and absence of pigment in vegetative parts.)
S. Black spotting on certain types of seed coat.
T. Less dense speckling, characteristic of the Taylor variety.
U. Buff, or clay-colored, seed coat.
W. Whippoorwill type of seed-coat spotting.
X. Taylor inhibitor cancels (crosses out) the effect of *T*.

The eight factors *B*, *F*, *N*, *P*, *R*, *TF*, *U*, and *X*, either singly or in combination, give rise to the ten distinguishable seed-coat colors, purple, black, dull black, blue, coffee, maroon, buff, red, pink, and white. The factors *P*, *B*, *D*, *T*, and *F* and probably *S* belong to a linked group. The factors *D*, *T*, and *F* restrict the distribution of color pigments in the seed coat. Three independent eye factors *I*, *H*, and *E*, either singly or in combination, give rise to the five distinct types of eyes, Watson, Holstein, small eye, narrow eye, and very small eye.

Indications were found that when all of the pigment factors are absent, including factor *R*, there is a tendency for the seeds to be small, weak, or abortive.

The flower color has been found to be correlated with the coloration in the seed coat, joints, peduncles, stipules, and petioles (*16, pp. 282–283*).

Experiments reported by Haigh and Lochrie (*6*) indicate a progressive variation with age of a simple Mendelian ratio in the cowpea. The results in the F_2 cultures from successive days of flowering showed an orderly variation in the simple Mendelian 3:1 ratio, an

excess of recessives in the first 9 days being compensated for by an excess of dominants as the plants grew older. No cause for this phenomenon was discovered.

Hofmann (*9*), in experiments at the University of Illinois, found that crosses made in the greenhouse between California Blackeye and Blue Goose show definite evidence of hybrid vigor.

Bonavist

(*Dolichos lablab* L.)

In studying *Dolichos lablab*, Harland (*8*) found that dehiscence of the anthers takes place at least 1 and sometimes 2 days before the flowers open. Studies in inheritance showed that in the case of determinate and indeterminate growth the segregating ratio in the F_2 generation was 3 : 1, with complete dominance of the indeterminate factor.

Two factors were found to influence color, each being transmitted independently, resulting in the expected 9 : 7 ratio. One of these factors has no effect except in the presence of the other, when it converts white flower into purple, and brown seed into black, and causes pigmentation of the nodal region.

Lupine

(*Lupinus* spp.)

Burlingame (*2*) reports studies of *Lupinus* species with reference to variation and inheritance. His findings show that races with dark-blue and pink flowers breed true and that races with striped white flowers are heterozygous for a single factor, which in the homozygous condition produces white flowers. Light-blue flowers are due to a single dominant factor, indistinguishable in the homozygous and heterozygous condition.

Dark seed coats are linked with dark-blue flower color, but probably due to separate factors.

The factors for light-blue and striped-white flowers are both allelomorphic to that for dark-blue and not improbably constitute a system of multiple allelomorphs.

Mutations are frequent, some are already known to be dominant, and others appear to be in the nature of additions of new characters and factors and so progressive in the sense of de Vries (*2, p. 447*).

Hallqvist (*7*) studied seven different types of flower color and five types of seed color in *Lupinus angustifolius* L. His conclusions were as follows (*7, p. 344*):

One fundamental colour factor has been demonstrated (pure red). A synthesis of blue colour has been obtained from crosses between bluish red and violet flower colours. One "dilution" factor has been found to be present.

Pleiotropic correlation has been demonstrated between certain flower and seed colours.

Three flower colour factors have been found to form a linkage group. The linkage between two of the factors is very close, if not complete. The other linkage value represents a crossover percentage of about 22%.

Greb (*5*), in studying *Lupinus albus* L., found that there are at least two genetically different rootlet types in this species. These differ in rate of rootlet elongation in young seedlings and in time of development of the root hairs. The ratio in the F_2 was 2:1, which suggested that the homozygous nonhairy might be lethal.

Adzuki Bean

(*Phaseolus angularis* (Willd.) Wight)

Kakizaki (*12*), in a study of crosses between Miyako and Donsu varieties of adzuki bean, found that reddish purple in the stems, black spotting on red seed coats, and blackish brown in ripe pods were dominant over their recessive allelomorphs, green stems, unspotted seed, and brown pods. From the segregating ratios in the F_2 it was concluded that color of stem was due to the interaction of two factors, while the black spotting of the seed coat and color of ripe pods were influenced by only one factor pair.

Colored stems are completely correlated with black-spotted seed coats, and colorless (green) stems with unspotted seed coats.

The factor *P* for reddish-purple color of stems and its recessive allelomorph *p* (green stems) are very closely linked with *S*, a factor for black-spotting of seed-coats, and its recessive allelomorph *s*, respectively, and hardly any crossing over occurs between them.

The *I* factor, which intensifies the purple color of the stem, and its recessive allelomorph *i* are also very closely linked with the *B* factor, which produces a blackish-brown color of the ripe pods, and *b*, its recessive allelomorph, and this linkage is also very close, so that crossing over hardly ever occurs between them.

The *P*-*S* linkage group is independent of the *I*-*B* linkage group.

Presence of *S* in a homozygous condition produces more intense spotting of the seed coats than when it is present in a heterozygous condition (*12, p. 177*).

Horsebean

(*Vicia faba* L.)

The horsebean is known to cross readily but has been used comparatively little in inheritance studies. Darlington (*3*) studied variegation and albinism and found that variegation is a heterozygous type of which albino and normal are the homozygous types. Sirks (*15*) in a study of quantitative inheritance in *Vicia faba* presented evidence to indicate that quantitative factors do exist.

Velvetbean

(*Stizolobium* spp.)

Several species of *Stizolobium* have been hybridized. Inheritance studies made at the Florida Agricultural Experiment Station a number of years ago were reported in the annual reports of that station for 1910, 1912, 1913, and 1915. Species that have been hybridized are *S. deeringianum* Bort × *S. pachylobium* Piper and Tracy, *S. deeringianum* × *S. niveum*, and *S. deeringianum* × *S. hasjoo*.

The inheritance studies are concerned mostly with the cross *S. deeringianum* × *S. niveum*, which are the species of most economic significance. In these crosses Belling (*1*) found that color in wings and standard, length of seed, curve in pods, and open and closed pods were influenced by a single factor pair, and size of pod and length of pubescence on pod by two or more factors, while mottling was due to three independent factors. Correlations were established between lateness of flowering and number of flowers in a raceme and between length of pod and seed.

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PIGEONPEA

(*Cajanus indicus* Spreng.)

Inheritance studies with the pigeonpea carried on at the Hawaiian Agricultural Experiment Station have been reported by Krauss (*14, p. 13*). According to his findings—

* * * red flower standards are dominant over yellow; blotched or speckled seed dominate over solid colored, and maroon-blotched pods are dominant over solid light-tinted pods. Pubescent pods are dominant over glabrous; large, flat pods are dominant over small round pods, and large seeds over small seeds. Four and five seeded pods are dominant over 3 and 4 seeded pods. Round seeds, slightly flattened, dominate over all others of widely different shapes, including spherical, oval, flattened, and irregular. The axillary flowers and pods dominate over terminal inflorescence. In stature blended inheritance is observable, very dwarf varieties when crossed with very tall varieties produce an intermediate type, and two varieties when crossed almost invariably produce a type that is taller and more vigorous than either parent. Crossing an annual type on a perennial type appears to produce perennial forms. This behavior has been found to remain constant, practically complete dominance for some well-defined differentiating unit characters being the rule.

When red dorsal standard sorts were crossed with red types, it was noticed that the solid red changed to red lacing, and when extremely tall and dwarfed forms were crossed, the first generation was of intermediate height. Wherever dominance is apparent the second generation shows fairly definite Mendelian segregation as well as definite linkage between some characters. Dihybrid crosses appear to adhere rather closely to the 9:3::3·1 ratio.

Studies in *Cajanus indicus* relating the inheritance of color in the flower and seed coat have been reported by Dave (*4*). In most cases one factor pair controlled color inheritance, but in others two independently inherited factors were operative, in agreement with the general results obtained by Kraus. Complete linkage was noted between orange-yellow flowers and purplish-black seed, yellow flowers and back of standard with purple veins, and base diffused purple and green pods; and purple color at the back of the standard was closely linked with maroon color of the pod.

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APPENDIX

Table 1.—*Chromosome numbers in legumes*

Name [1]	Chromosome numbers [2]		Reference no.
	n	2*n*	
Acacia arabica Willd		±52, ±104	[3] *(26)*, *(28)*
A. baileyana F. Muell	13		*(59, 60)*
A. cyanophylla Lindl		26	*(26, 28)*
A. dealbata Link		26	*(26, 28)*
A. decurrens Willd		26	*(27, 28)*
A. dermatophylla F. Muell. [Benth.]	13	26	*(15)*
A. eburnea Willd		±52, ±104	*(27, 28)*
A. farnesiana Willd		±52, ±104	*(26, 28)*
A. horrida Willd		±52, ±104	*(26, 28)*
A. longifolia Willd		26	*(27, 28)*
A. lophantha		24	*(74)*
A. nilotica		±52, ±104	*(26)*
A. podalyriaefolia A. Cunn		26	*(26, 28)*
A. saligna Wendl		26	*(27)*
A. scorpioides A. Chev., var. *adstringens* (Schum. and Thon.) A. Chev		52, 104, 208	*(27, 28)*
A. scorpioides A. Chev., var. *nilotica* Benth		±52, ±104	*(28)*
A. scorpioides A. Chev., var. *pubescens* Benth		±52, ±104	*(27, 28)*
Aeschynomene indica L	20		*(44)*
Amorpha californica Nutt	10		*(48)*
A. fruticosa L	20		*(48)*
Do		40	*(48)*
A. microphylla Pursh	10		*(48)*
Amphicarpa monoica (L.) Ell	10		*(11)*
Anthyllis alpestris Kit		12	*(7)*
A. barba-jovis L		14	*(7)*
A. gerrardi L		16	*(7)*

[1] Names are given as in the articles cited except for obvious misspelling. Where the wrong authority for a name is given it is followed by the correct authority in brackets.

[2] Letters following numbers denote number of times verified by other authors. c=1; d=2; e=3; f=4; g=5; h=6; j=8, k=9; s=17; t=18.

[3] Italic numbers in parentheses refer to References for Chromosome Numbers. In the case of more than 1 determination, the earliest author giving the established number is listed.

TABLE 1 —*Chromosome numbers in legumes*—Continued

Name	Chromosome numbers *n*	Chromosome numbers 2*n*	Reference no
A maritima Schweigg		12	(7)
A tetraphylla L		16	(7)
A vulneraria	6	12	(14)
Arachis hypogaea L	20e	40e	(44)
A hypogaea (Spanish and small Japan peanuts)	10		(35 pp 338–342)
A nambyquare		40	(37)
A prostrata Benth var *rasteiro*		±40	(28)
A rasteiro Chevalier (?)		40	(38)
Astragalus alopecuroides L	8		(48)
A altaicus Bunge		16	(4)
A baeticus L	8		(47)
A candidissimus Led		16	(4)
A echinus DC		64	(4)
A edulis Dur	[a] 14		(48)
A exscapus B *transsilvanicus* A and G = *A transsilvanicus* Barth		16	(4)
A falcatus Lam	8		(47)
A galegiformis L	8		(47)
A hamosus L	24		(48)
Do		48	(4)
A hypoglottis L		16	(4)
A massiliensis Lam		16	(48)
A membranaceus Fisch [Bunge]		16	(4)
A mollis	8		(48)
A monspessulanus L	8		(47)
A secundus DC		48	(66)
A sesameus L	8		(47)
Do		16	(4)
A sieversianus Pall		16	(4)
A sinicus L	8		(44)
Do		16	(74)
A transsilvanicus		16	(4)
A vulpinus Willd	8		(47)
Baptisia australis R Br	9		(71)
B australis R Br var *exalta* Sweet		18	(5)
B sulphurea Engelm	9		(71)
B tinctoria R Br		18	(5)
Biserrula pelecinus L	8		(47)
Cajanus indicus Spreng	11		(62)
Calophaca wolgarica Fisch	8		(47)
Canavalia ensiformis DC	11		(44)
C gladiata DC		22	(7)
Caragana arborescens Lam		16	(7)
C frutescens DC		32	(4)
Carmichaelia australis R Br	1		(48)
Cassia didymobotrya	14	28	(70)
C dimidiata		16	(74)
C fistula	12		77 pp 541–623
C leschenaultiana DC	24		(44)
C mimosoides L	8 16		(44)
C occidentalis L	13		(56)
C purpurea Roxb	10		(31)
C sophera L	12		(44)
C tomentosa L	12e		(38)
C tora L	13		(16)
Cercis siliquastrum	7	14	(13)
Cicer arietinum L	7		(17)
Do		14e	(18)
Do		16	(55)
C kabulium	8	16	(17)
Clitoria ternatea L		16	(7)
Colutea arborescens L		16	(4)
C halepica Lam	8		(48)
C media Willd (*C arborescens* L × *C orientalis* Lam)	8		(48)
C orientalis Lam	8		(48)
Crotalaria alata Ham	8		(44)
C anagyroides H B K	8		(44)
C arenaria Benth	8		(32)
C juncea		16	(2)
C obovata G Don	8		(32)
C retusa L	8	16	(44)
C usaramoensis Back [Baker]	8		(44)
C valetonii Back	8		(44)

[a] Approximately

TABLE 1 —*Chromosome numbers in legumes*—Continued

Name	Chromosome numbers		Reference no
	n	*2n*	
Cyamopsis psoraloides DC	7	14	(6?)
Cytisus canariensis O Kuntze		46	(5)
C nigricans L	24		(81)
Do		48	(5)
C purpureus		48	(73)
C scoparius Link	24c		(44)
C scoparius		48	(74)
C sessilifolius L		52	(5)
Desmodium grandiflorum (Walt) DC	11		(11)
D perpesum DC [5]	11		(44)
Dolichos biflorus		24	(63)
D lablab L	11c		(78)
Do		22	(41)
Do		24	(63)
D lubia Forsk		22	(7)
D multiflorus		24	(58)
D niloticus Del		22	(7)
D ornatus Wall		22	(7)
Dorycnium herbaceum Vill		14	(7)
D hirsutum Ser		14	(7)
D rectum Ser		14	(7)
D suffruticosum Vill		14	(7)
Erythrina crista galli L		44	(7)
Galega officinalis L	8		(47)
Do		16	(4)
G orientalis Lam	8		(47)
Genista ferox Poir		48	(5)
G pilosa L		24	(5)
G sagittalis L		44(42–45)	(5)
G tinctoria v *angustifolia* Ledeb		48	(5)
G triangularis Kit		48(48–50)	(5)
Glycine gracilis Skvortzow	20	40	(24)
G hispida		38	(30)
G hispida Max	20	40	(24)
G soja Sieb and Zucc	20c	40d	(44)
G soja var *akasaya*		38	(86)
G ussuriensis		40	(7)
Glycyrrhiza aspera Pall		16	(4)
G echinata L	8		(47)
G uralensis Fisch		16	(4)
Hedysarum elongatum Fisch var *albiflorum* Ledeb		14	(66)
Hymenocarpus circinnatus Savi		16	(7)
Indigofera aspera Perr	8		(32)
I decora Lindl		48	(4)
I diphylla	8		(32)
I gerardiana Wall	24		(47)
I kirilowi Maxim	8		(44)
I parviflora Heyne	7		(32)
I pseudotinctoria Matsum	8		(44)
I pseudotinctoria		16	(74)
I suffruticosa Mill	16		(44)
I sessiliflora DC	16		(32)
I viscosa Lam	8		(32)
Laburnum adami		48	(79)
L alpinum Griseb		48(50)	(5)
L vulgare		48	(79)
Lathyrus angulatus L	7		(71)
L annuus L	7		(71)
L aphaca L	7c		(19)
L articulatus L	7c	14c	(14)
L cicera L	7c	14	(13)
L cirrhosus Ser	7		(71)
Lathyrus clymenum L	7		(71)
Do		[4] 14	(59)
L crassipes Gillies		14	(69)
L dumetorum Philippi		14	(69)
L ensifolius Bad	7		(71)
L grandiflorus Sibth and Sm	7c	14	(14)
L heterophyllus L	7		(71)
L hirsutus L	7		(71)
L latifolius L	7c	14	(84)
L macropus Gillies		14	(69)
L magellanicus Lam		14	(53)
L maritimus Bigel	7c		(44)

[4] Approximately

[5] Apparently name is wrong.

Table 1.—*Chromosome numbers in legumes*—Continued

Name	Chromosome numbers		Reference no.
	n	2*n*	
L. niger	7c	14c	(*15*)
L. nigrivalis A. Burkart		14	(*69*)
L. nissolia L.	7		(*71*)
L. numidicus Batt.	7		(*71*)
L. ochroleucus Hook.		14	(*69*)
L. ochrus DC.	7c	14	(*13*)
L. odoratus L.	7h	14d	(*84*)
L. palustris	7		(*69*)
L. pannonicus L. [Garcke]		14	(*53*)
L. paranensis A. Burkart		14	(*69*)
L. parodii A. Burkart		14	(*69*)
L. pratensis L	7	14	(*53*)
L. pubescens Hook. and Arnot	7		(*71*)
L. quadrimarginatus Bory and Chaub.		14	(*69*)
L. rotundifolius Willd.	7		(*71*)
L. sativus L.	7d	14	(*14*)
L. sessifolius Hook. and Arnot		14	(*69*)
L. setifolius L	7		(*69*)
L. sylvestris L	7		(*71*)
Do		14	(*53*)
L. sphaericus Retz	7		(*71*)
L. tingitanus L	7c	14	(*53*)
L. tuberosus L	7		(*21*)
L. venosus Muhl		28	(*69*)
L. vernus Bernh.	7		(*71*)
Do		14c	(*68*)
Lens esculenta Moench	7		(*78*)
Do		14f	(*68*)
Lespedeza bicolor Turcz.	9		(*44*)
L. cyrtobotrya Miq	9		(*44*)
L. daurica Schindl		36	(*11*)
L. homoloba Nakai	9		(*44*)
L. sericea Benth		18	(*11*)
L. sieboldi Miq	9		(*44*)
L. stipulacea Maxim		20	(*11*)
L. tomentosa Siebold		20	(*11*)
L. variegata Cambess		18	(*11*)
Lotus angustissimus L		12	(*7*)
L. corniculatus L		12c	(*45*)
L. corniculatus L. var. *alpestris* Lamotte		24	(*7*)
L. corniculatus L. var. *japonicus* Regel	6c		(*44*)
L. creticus L		28	(*7*)
L. cytisoides L		14	(*7*)
L. filicaulis Dur		12	(*7*)
L. hispidus Desf		24	(*7*)
L. ornithopodiodes L		14	(*7*)
L. requieni Mauri		14	(*7*)
L. siliquosus L		14	(*7*)
L. tetragonolobus L		14	(*7*)
L. uliginosus Schkuhr		14	(*7*)
Lupinus albicoccineus		48	(*79*)
L. albus L		50	(*79*)
Do		[4] 40	(*72*)
L. angustifolius L	20		(*85*)
Do	24		(*44*)
Do		40c	(*61*)
L. barkeri Lindl		50c	(*5*)
L. densiflorus Benth		48	(*79*)
L. douglasii Agar		48	(*79*)
L. elegans H. B. and K. T. H		48	(*79*)
L. hartwegii Lindl		48–50	(*79*)
L. hirsutus L. var. *micranthus* Boiss		50	(*79*)
L. luteus L	[4] 23		(*78*)
Do	24		(*44*)
Do		44–45	(*33*)
Do		46	(*61*)
L. micranthus Dougl		48	(*79*)
L. mutabilis Sweet	24		(*85*)
Do		42	(*54*)
Do		48	(*79*)
L. nanus Dougl		48	(*79*)
L. ornatus Dougl		48	(*79*)
L. pilosus L. [Murr.]		42	(*79*)
L. polyphyllus Lindl	24		(*11*)

[4] Approximately.

TABLE 1.—*Chromosome numbers in legumes*—Continued

Name	Chromosome numbers		Reference no.
	n	2*n*	
L. polyphyllus Lindl.		48	(*79*)
L. pubescens Benth.		48	(*79*)
L. subcarnosus Hook.		36	(*79*)
L. succulentus		48	(*79*)
L. varius L.		48	(*5*)
L. venustus Vilm.		48	(*79*)
Medicago apiculata Willd.		16	(*29*, *28*)
M. arabica All.		16c	(*25*)
M. arborea L.		32	(*29*, *28*)
M. carstiensis Wulf.		16	(*25*)
M. ciliaris Krock.		16d	(*29*, *28*)
M. coronata Desr.		16	(*25*)
M. denticulata Willd.		16	(*29*, *28*)
M. disciformis DC.		16	(*29*, *28*)
M. dzhawakhetica Bordz.		16	(*11*)
M. echinus DC.		16c	(*25*, *28*)
M. falcata L.	16		(*78*)
Do.		16	(*25*)
Do.		32d	(*29*, *28*)
M. gerardi Waldst. and Kit.		16	(*29*, *28*)
M. glutinosa M. Bieb.		32	(*11*)
M. helix Willd.		16	(*25*, *28*)
M. hemicycla Grossh.		32	(*11*)
M. hispida		14c	(*25*)
M. intertexta Mill.		16c	(*25*)
M. laciniata Mill.		16d	(*29*, *28*)
M. lappacea Desr.		16	(*29*, *28*)
M. littoralis Rhode		16c	(*29*, *28*)
M. lupulina L.	8c		(*78*)
Do.		16d	(*25*, *28*)
M. lupulina typica Urban		32	(*6*)
M. maculata Willd.		16	(*25*, *28*)
M. marina L.		16	(*29*, *28*)
M. media Pers.		32, 3[illegible]	(*25*)
M. minima L.		16c	(*25*, *28*)
M. murex Willd.		16d	(*29*, *28*)
M. muricata (L.) All.		16	(*23*)
M. nigra Krock.		16	(*29*, *28*)
M. obscura Retz.		16, 17 or 18	(*25*)
M. olivaeformis Guss.		16	(*29*, *28*)
M. orbicularis All.		16d	(*25*, *28*)
M. ovalis Urban (syn. *Trigonella ovalis* Boiss.)		32	(*6*)
M. pentacycla DC.		16	(*29*, *28*)
M. platycarpa (L.) Trautv.	8		(*78*)
Do.		16c	(*25*)
M. radiata L. (syn. *Trigonella radiata* Boiss.)		16	(*6*)
M. rigidula DC.		16	(*25*, *28*)
M. rigidula (L.) Desr.		14	(*25*)
M. rotata Boiss.		16	(*25*)
M. rugosa Desr.		32	(*25*)
M. ruthenica Trautv.		16	(*25*)
M. sativa L.	16d		(*78*)
Do.		32g	(*19*)
M. scutellata Mill.		32c	(*25*, *28*)
M. soleirolii Duby		16	(*25*)
M. sphaerocarpa Bertol.		16	(*25*, *28*)
M. tenoreana Ser.		16	(*25*, *28*)
M. tornata Mill.		16	(*25*, *28*)
M. tribuloides Desr.		16	(*29*, *28*)
M. truncatula Gaertn.		16	(*25*, *28*)
M. tuberculata Willd.		16d	(*29*, *28*)
M. turbinata Willd.		16c	(*29*, *28*)
Melilotus alba Med. [Desr. (?)]	8d	16g	(*19*)
M. dentata Pers.		16	(*6*)
M. indica All.		16c	(*25*)
M. italica (L.) Lam.		16	(*8*)
M. melilotus indica A. and G. (syn. *M. parviflora* Desf.)		16	(*6*)
M. messanensis All.		16	(*8*)
M. neapolitana Ten. (syn. *M. gracilis* DC.)		16	(*6*)
M. officinalis	8		(*10*)
Do.		16e	(*19*)
M. segetalis Ser.		16	(*8*)
M. speciosa Dur.		16	(*9*)
M. suaveolens Ldb.		16	(*6*)
M. sulcata Desf.		16d	(*25*)

TABLE 1.—*Chromosome numbers in legumes*—Continued

Name	Chromosome numbers		Reference no.
	n	*2n*	
M. taurica Ser.		16	(*6*)
M. wolgica Poir.		16c	(*6*)
Millettia japonica A. Gray	8		(*44*)
Mimosa pudica L.	24		(*44*)
Onobrychis crista-galli Lam.	7	14	(*14*)
O. viciaefolia Scop.	11		(*12*)
Do		22	(*61*)
Ononis alopecuroides L.		32	(*6*)
O. biflora Desf.		32	(*6*)
O. fruticosa L.		32	(*6*)
O. hircina Jacq.		32 (30)	(*6*)
O. natrix L.		32	(*6*)
O. ornithopodiodes L.		32	(*6*)
O. reclinata L.		64	(*6*)
O. rotundifolia L.		32	(*6*)
O. spinosa L.		32 (30)	(*6*)
O. viscosa L.		32	(*6*)
Ornithopus sativus Brot.	8	16	(*44*)
Oxytropis halleri Bunge		16	(*4*)
O. rishiriensis Matsum.		[4] 53	(*66*)
O. uralensis Pall. [DC.]		16	(*4*)
O. vaginata Fisch.		16	(*4*)
Pachyrhizus angulatus	11		(*65*)
Parochetus communis		16	(*12*)
Phaseolus aconitifolius Jacq.		22	(*7*)
P. acutifolius A. Gray		22	(*41*)
P. angularis Willd. [(Willd.) W. F. Wight]		22	(*41*)
P. aureus Roxb		22	(*41*)
P. capensis Thunb.		22	(*7*)
P. chrysanthos Sav.	11	22	(*56*)
P. lunatus L.	11		(*44*)
Do		22	(*41*)
P. multiflorus Willd.	12		(*46*)
Do		22c	(*41*)
P. mungo L.		22	(*41*)
Do		24	(*63*)
P. nigerrimus Juss.		22	(*7*)
P. radiatus L.	11		(*43*)
Do		22c	(*43*)
Do		24	(*63*)
P. trilobus		22	(*41*)
P. vulgaris L.	11		(*44*)
Do		22g	(*41*)
Piptanthus nepalensis Sweet		18	(*5*)
Pisum arvense L.	7c		(*85*)
Do		14	(*51*)
P. elatius Bieb.	7	14	(*51*)
P. fulvum Sibth. [Sibth. and Sm.]	7	14	(*51*)
P. humile Boiss. [Boiss. and Noë]	7	14	(*51*)
P. jomardi Schrank	7	14	(*51*)
P. sativum L.	7s	14t	(*3*)
Psoralea bituminosa L.	10		(*48*)
Do		[4] 20c	(*47*)
P. glandulosa L.		[4] 20	(*47*)
P. macrostachya		20	(*48*)
P. palaestina L.		[4] 20	(*47*)
Rhynchosia phaseoloides DC.		22	(*7*)
Robinia boyntonii Ashe	15		(*83*)
R. fertilis Ashe	10		(*83*)
R. hartwigii Koehne	10		(*83*)
R. hispida L.	15		(*83*)
Do		30	(*48*)
R. kelseyi Hutchins	10		(*83*)
R. luxurians (Dieck) Schneid.	10		(*83*)
R. pseudoacacia L.	10		(*47*)
Do		22	(*4*)
R. viscosa Vent.	10		(*83*)
Securigera coronilla DC.		12	(*7*)
Sesbania aculeata Pers.	16		(*44*)
Soja hispida Mönch		40	(*41*)
S. max, Illini variety	20	40	(*80*)
Sophora angustifolium Sieb. and Zucc.	9		(*44*)
S. chinensis G. [G. Don]		28	(*5*)

[4] Approximate.

TABLE 1.—*Chromosome numbers in legumes*—Continued

Name	Chromosome numbers n	Chromosome numbers 2n	Reference no.
S. davidii Kom.		16	(*5*)
Sophora flavescens Ait.		18	(*5*)
S. japonica L.		28	(*5*)
S. moorcroftiana Benth.		16	(*49*)
Spartium junceum L.		48 (48–52)	(*5*)
Swainsonia galegifolia R. Br. var. *albiflora* Lindl.	16		(*11*)
Tephrosia hookeriana Wt. and A.	16		(*44*)
Thermopsis alterniflora Regel [Regel and Schmalh.]		18	(*5*)
T. montana Nutt.	9		(*71*)
Do.		18	(*5*)
Trifolium albopurpureum T. and G.		16	(*82*)
T. alexandrinum		16	(*82*)
T. alpestre L.	8		(*1*)
Do.		16	(*42*)
T. ambiguum M. B.		16	(*42*)
T. angustifolium L.		14	(*42*)
T. arvense L.	–		(*1*)
Do.		14	(*42*)
T. badium	7		(*1*)
T. campestre	–		(*1*)
T. ciliolatum Benth. (*T. ciliatum* Nutt.)		16	(*82*)
T. dichotomum H. and A.		32	(*82*)
T. filiforme L.		14	(*42*)
T. fragiferum L.	8		(*1*)
Do.		16	(*42*)
T. fucatum Lindl.		16	(*82*)
T. glomeratum	–		(*1*)
Do.		16	(*82*)
T. hybridum L.	8c		(*1*)
Do.		16d	(*42*)
T. incarnatum L.	8		(*1*)
Do.		14d	(*42*)
Do.		16	(*61*)
T. lappaceum L.	8		(*1*)
Do.		16	(*42*)
T. lupinaster L.		48	(*42*)
T. maritimum Huds.		16	(*42*)
T. medium L.	[a] 48–49		(*1*)
Do.		[a] 80	(*42*)
T. microcephalum Pursh		16	(*82*)
T. minus	14		(*1*)
Do.		32	(*82*)
T. montanum L.	9 (?)		(*1*)
Do.		16	(*42*)
T. obtusiflorum Hook.		16	(*82*)
T. ochroleucum	8		(*1*)
T. pannonicum Jacq.	[a] 48–49		(*1*)
Do.		[a] 130	(*42*)
Trifolium parviflorum Ehrh.		16	(*42*)
T. pratense L.	7c		(*1*)
Do.	[a] 12		(*52*)
Do.		14d	(*42*)
Do.		(24)	(*61*)
T. procumbens L.		14	(*42*)
T. reflexum L.		16	(*82*)
T. repens L.	[a] 12		(*52*)
Do.	14		(*1*)
Do.	16		(*44*)
Do.		16	(*20*)
Do.		32d	(*42*)
Do.		(24) 28	(*61*)
T. resupinatum L.	8		(*1*)
Do.		16	(*42*)
T. rubens L.		16	(*42*)
T. scabrum L.		16	(*42*)
T. spadiceum L.		14	(*42*)
T. squarrosum L.		14	(*42*)
T. subterranea		16	(*82*)
T. thalii	8		(*1*)
T. tumens Stev.		16	(*42*)
T. variegatum Nutt.		16	(*82*)
T. wormskoeldii Lehm.		48(?)	(*82*)
Trigonella balansae Boiss. [Boiss. and Reut.]		16	(*76*)
T. calliceras Fisch.		16	(*76*)

[a] Approximate.

TABLE 1 —*Chromosome numbers in legumes*—Continued

Name	Chromosome numbers *n*	Chromosome numbers *2n*	Reference no
T coerulea (L) Ser		16	(29)
T corniculata L		16	(76)
T cretica (L) Desr		16c	(29)
T foenumgraecum L		16c	(29)
T glomerata Hort (syn *Medicago brachycarpa* Fisch)		16	(6)
T melilotus coerulea A and G (syn *Melilotus coerulea* Desf)		16	(6)
T monspeliaca L		16	(6)
T polycerata L		28	(6)
T striata L (syn *T cancellata* Desf)		16	(5)
Ulex europaeus L		96	(5)
U nanus Forst		46	(5)
U parviflorus Pourr		96	(5)
Vicia alpestris Steph (Stev)		28	(34)
V amoena Fisch	12		(78)
Do		24	(75)
V amphicarpa L	7	10	(76)
V angustifolia L	6	12d	(75)
V atropurpurea Desf	7		(75)
Do		14d	(68)
V aurantia Boiss		14	(34)
V bithynica L	7c	14d	(75)
V calcarata Desf		14	(34)
V cracca L	6c	12c	(67)
Do	7	14	(76)
Do	14		(78)
Do		28	(75)
V dasycarpa Ten	7	14c	(75)
V disperma DC	7	14d	(75)
V dumetorum		14	(34)
V erviformis Boiss		14	(34)
V ervilia Willd	7	141	(75)
V faba L	[illegible]		(50)
Do		12k	(57)
Do	7	14	(44)
V gracilis Lois	7		(78)
Do		14	(75)
V grandiflora Scop	7		(78)
Do		14c	(75)
V hirsuta S F Gray	7c	14d	(75)
V hybrida L	6	12c	(7[illegible])
V hyrcanica Fisch and Mey		12	(34)
V lathyroides L		12	(34)
V lutea L	7		(78)
Do		14c	(75)
V macrocarpa	6		(78)
Do		10	(34)
Do		12	(75)
V monantha Desf	7		(78)
Do		14d	(75)
V musquinez Bosc		14	(34)
V narbonensis L	7		(78)
Do		14d	(75)
V orobus DC	6		(78)
Do		12c	(7[illegible])
V pannonica Crantz	6	12c	(7[illegible])
Do	7		(78)
V peregrina L	7		(78)
Do		12	(34)
Do		14	(75)
V picta Fisch and Mey	7		(78)
Do		14	(75)
V pisiformis		12	(34)
V pseudocracca Bertol	7		(75)
Do		14c	(68)
V pseudoorobus		12	(68)
Do		14	(34)
V pyrenaica Pourr		14	(34)
Vicia sativa L	6d		(68)
Do	7		(44)
Do		12g	(39)
V sepium L	7	14d	(75)
V serratifolia Jacq	7		(78)
Do		14c	(75)
V sicula Guss		14	(34)
V silvatica L	7		(78)
Do		14	(75)

TABLE 1 —*Chromosome numbers in legumes*—Continued

Name	Chromosome numbers		Reference no
	n	2n	
V tenuifolia Roth	12		(78)
Do		24c	(75)
V tetrasperma Moench	7c		(78)
Do		14c	(75)
V unijuga A Br	6		(78)
Do	12		(68)
Do	18		(44)
Do		12c	(75)
Do		24	(39)
V villosa Roth	7		(78)
Do		14c	(75)
Vigna catjang (Burm) Walp		22	(41)
Do		24	(63)
V glabra Savi		22	(7)
V oahuensis Vog		22	(7)
V sesquipedalis A I Hierters [I Ascherih]	12		(44)
V sinensis Endl	12		(44)
V unguiculata (L) Walp		22	(41)
V vexillata Benth		22	(7)
Wistaria brachybotrys Sieb and Zucc	8c		(40)
W floribunda DC	8d		(40)
W frutescens (L) Poir	8		(64)
W macrostachya Nutt	8		(64)
W multijuga Van Houtte (*W chinensis* var *multijuga* Hook)		48	(4)
W sinensis Sweet	8		(64)
W venusta Rehder and Wilson	8		(64)

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BREEDING MISCELLANEOUS GRASSES[1]

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THE grass family, known by botanists as the Gramineae, is the most important and widely distributed of all plants. Grasses are found from the Tropics to the Arctic Zone, and in deserts and swamps. To this group belong some of the most important cultivated crops such as corn, wheat, oats, rye, barley, rice, sugarcane, and the sorghums and millets.

Grass breeding really began in a remote time with the development of these crops from various species of wild grasses. This breeding, however, had for its purpose an increased production of food grain rather than any improvement in forage value. Pastoral agriculture was founded on the utilization of grasslands for grazing domesticated animals; and primitive peoples still migrate, with their flocks, in search of grass which provides the entire sustenance of these animals. It is only within the last 30 years that any serious effort has been made to increase the forage production of grasses.

In different parts of the world natural selection took place under the influence of climate, and thus we find the original grasslands of each country characterized by certain genera and species, which are native or indigenous there. As civilization developed and intercourse between nations became easy, the native grasses of each country were introduced and domesticated in countries having similar climates, so that grasslands are now less distinctive from a national viewpoint than formerly. However, there still remain more or less well-defined centers of development for each of the important grasses, and these centers are important as sources of breeding material.

GERM-PLASM SOURCES FOR VARIOUS GRASSES

GROUPS of related grasses have become concentrated in certain parts of the world as a result of their reactions to climatic conditions. It is in such regions that these genera are found in the greatest abundance, and here also the widest variation may be expected in habit of growth within the species. These development centers have been outlined broadly in figure 1, which may be considered as a graphic illustration of grass adaptations and the chief grass resources of the world, with the natural migration channels of these grasses indicated, of course, without any attempt to present details. The most important genera

[1] The purpose of this article is to bring together as far as possible the available information as to the breeding in progress and that contemplated with all grasses of agricultural importance with the exception of timothy, sugarcane, and the cereal grasses such as corn, sorghum, rice, wheat, rye, oats, and barley. As considerable breeding work has been done with timothy, it is discussed in a separate article.

[2] Died Feb. 22, 1937.

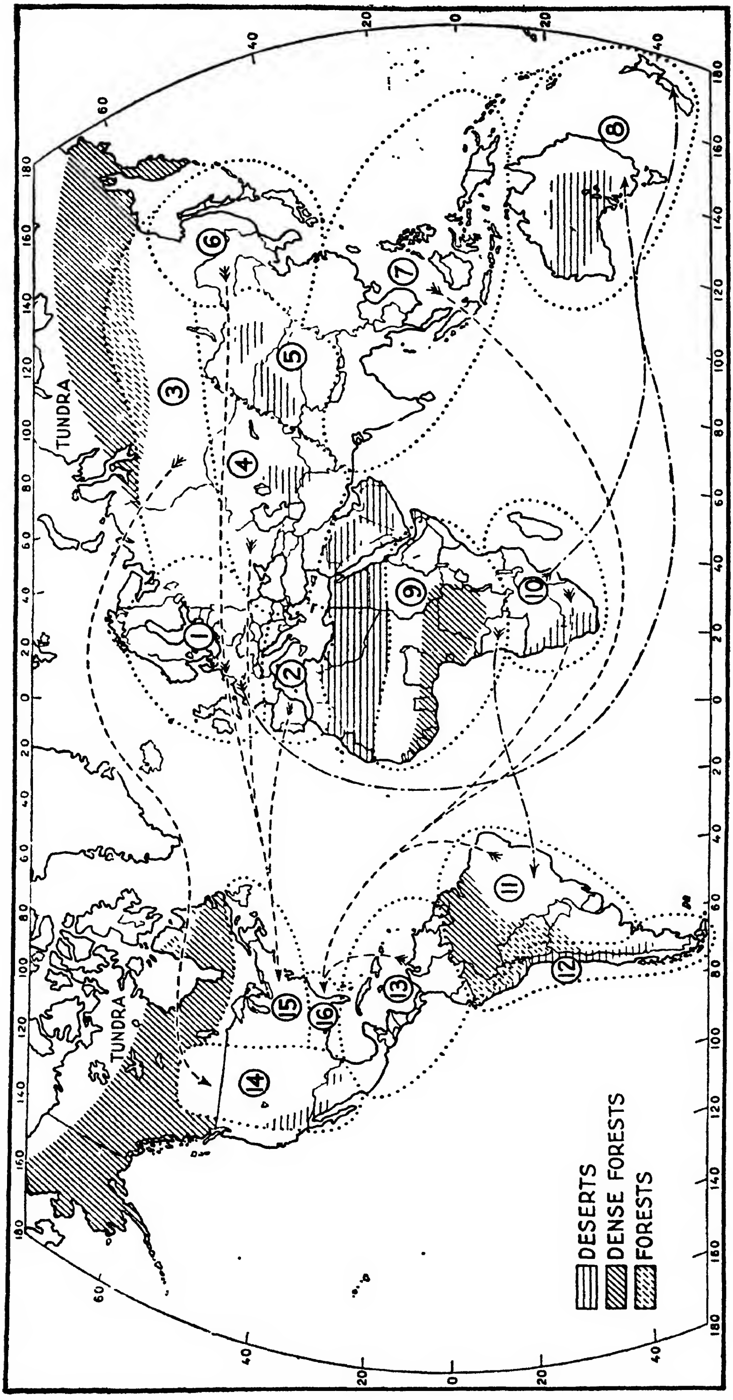

Figure 1.—Development centers of various important grasses.

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and species in each of the 16 regions are listed in table 1 (in the appendix). The boundaries or limits of these regions are obviously not exact, and wide variations occur within certain regions because of mountain ranges and other physiographic features that affect vegetation.

Region 1 includes most of western Europe where the annual precipitation is 20 inches or more and the temperatures are mild. Practically all of the so-called "tame" grasses now grown in southeastern Canada and the humid part of the United States north of the Cotton Belt are native in region 1 and were introduced from there by early settlers in North America. This region is rich in species and varieties of timothy, bluegrass, orchard grass, ryegrass, redtop, bentgrass, oatgrass, and fescue. Other grasses abundant in this region, but of little or no agricultural value, are velvet grass (*Holcus lanatus*),[3] matgrass (*Nardus stricta*), and the other moorland grass (*Molinia caerulea*). These constitute the principal grass cover of wet heaths and moorlands throughout this region.

Region 2, the Mediterranean region of Europe and Africa, characterized by low rainfall and rather poor soils, is the native home of the annual species of *Avena* (wild oats), bromes, and fescues. Most of the winter annual grasses now growing in the foothills of southern Cali-

[3] The authorities for the botanical names used in this article are given in table 5 of the appendix.

COMPARED *with the work in several other countries, very little has been done in the United States in breeding any of the grasses except timothy. Orchard grass, bluegrass, redtop, bromegrass, bentgrass, Bermuda grass, carpet grass, and all other grasses ordinarily used in seeding pastures and lawns are mixed populations consisting of many strains that vary in such important characteristics as date of maturity, disease resistance, leafiness, number and vigor of stolons and rhizomes, and viability and abundance of seed. Because of these wide variations, there is a great opportunity for improvement by simple selection processes, and probably still greater possibilities in hybridization. The widely differing uses of grass, however, necessitate a close scrutiny and thorough examination of the variants from the standpoint of each possible use. Moreover, improved strains developed by British or other foreign workers are not likely to represent the best for our own country, since maximum values in plant breeding are attained only by aiming for close adaptation to local conditions. In the development of improved grasses, we shall have to solve our own problems by a systematic attack based on regional differences.*

fornia are of Mediterranean origin. In addition red fescue, canary grass, and Harding grass originated in region 2. The esparto or alfa grass used in the manufacture of fine paper grows naturally in northern Africa. Grasses that are abundant in this region but of little value include many species of both *Aristida* and *Stipa*.

Region 3 includes the eastern or low-rainfall section of the Union of Soviet Socialist Republics and practically all of Siberia. Here, where the average rainfall is less than 20 inches and the winters are very severe, a group of extremely hardy and drought-resistant grasses has developed, including the crested wheatgrass which has proved so valuable on the northern Great Plains of the United States. On the dry, cold steppes are many species and varieties of wheatgrass (*Agropyron*), wild-rye (*Elymus*), reedgrass (*Calamagrostis*), and "chee" or "tshee" grass (*Stipa*). The small fescues such as the sheep fescue are present but not so characteristic of this region as the Agropyrons.

Region 4, including southeastern Union of Soviet Socialist Republics, western China, and that ancient cradle of the human race, Asia Minor, Persia, and Afghanistan, is peculiarly important as the native home of several cereal grasses. All of this region is very dry and a considerable part is actual desert. While not so important from a forage standpoint, the native grasses of this region include what are believed to be the progenitors of wheat, emmer, einkorn, and rye. Numerous species of wheat (*Triticum*), rye (*Secale*), and their near relatives the goatgrasses (*Aegilops* and *Haynaldia*) are found here. The wild barleys (*Hordeum* spp.) are common, and bulbous bluegrass (*Poa bulbosa*) is almost everywhere. Meadow foxtail, sweet vernalgrass, red fescue, and Johnson grass are other important grasses found in region 4.

Region 5 includes Tibet, the western provinces of China, and eastern Mongolia. This is a region of high mountain ranges, cold, dry plateaus, and deserts. On account of its inaccessibility less is known about the grasses of this region than of any other part of the world. The grasses that have developed here would assuredly be drought-resistant and able to withstand other climatic extremes. At least four species of bluegrass and as many fescues have been reported from this region, along with several species of wheatgrass and wild-rye. Needlegrass (*Stipa* spp.) and sedges (*Carex* spp.) are widely distributed.

Region 6 includes eastern Siberia, Manchuria, northeastern China, Chosen, and Japan. Although attention has chiefly been given to the many soybean varieties in this region, it is also important as the home of most of our cultivated millets and that group of sorghums known as kaoliang. Foxtail millets, broomcorn millet (proso), and Japanese millet are all widely distributed and show a great variety of forms in this region. The Japanese lawngrass (*Zoysia japonica*) and Manila grass (*Zoysia matrella*), both of which appear valuable in the United States, are at home here. Among the less important grasses are many species of *Arundinella*, *Calamagrostis*, *Ischaemum*, and *Panicum*.

Region 7, including southeastern China, most of India, Burma, the Malay Peninsula, and adjacent islands, is largely tropical and has a heavy rainfall except in northern India. Such important cultivated crops originated in this region as sugarcane, rice, and bamboo; and also the forage grasses, Bermuda grass, Angleton grass, and centipede

grass. There are many other species and varieties of *Andropogon*, *Cynodon*, *Eleusine*, *Oryza*, *Panicum*, *Paspalum*, *Saccharum*, and *Sorghum* that have not yet proved of value under cultivation but may be of some importance from a breeding standpoint. Cogon grass, said to be a useful pasture grass in China and the Philippine Islands, is of doubtful value in the United States on account of its aggressive rootstocks.

Region 8, including Australia, New Zealand, and Tasmania, has a very distinctive vegetation, and many of the native grasses of this region are found nowhere else in the world except in small experimental plantings. The interior of Australia is very dry, almost desertlike. Along the coast where rainfall conditions are favorable the pastures and meadows are composed almost entirely of grasses and legumes introduced from Europe. In the drier portions native grasses supply most of the forage, and the most important of these are perhaps Mitchell grass, Wallaby grass, kangaroo grass, red grass (*Themeda* sp.), Flinders grass, and tussock grass. On the sand ridges in the semidesert area spinifex (*Triodia* spp.) is very abundant. Common Mitchell grass, curly Mitchell grass, and Wallaby grass have all been introduced into the United States, but they seem to be of little value here. The tussock grass of New Zealand (*Poa flabellata*) appears to be a very desirable grass, but so far all attempts to introduce it have failed. So much of Australia is desertlike that many grasses such as the annual bromes, fescues, Avenas, and Hordeums, which are not considered desirable in the United States, are appreciated there.

Region 9 consists of the equatorial part of Africa, some of which is occupied by dense forest. In parts where the rainfall is not too heavy, grasses abound in the open places of the timbered areas and in exclusively grass-covered lands or savannas replete with wild game animals. Here are found numerous species of *Sorghum*, *Pennisetum*, *Panicum*, *Hyparrhenia*, *Andropogon*, *Ehrharta*, and *Themeda*. Molasses grass and jaragua grass originated here, but are now more important in South America. In the highlands of Ethiopia are found many Hordeums (barley relatives). Sudan grass originated near Khartum, and other varieties of grass sorghum occur in profusion in this region. Pearl millet is native here also and originally was an important food crop of the inhabitants.

Region 10 is composed of that part of Africa south of 10° S. latitude and the adjacent island of Madagascar. The annual rainfall varies from about 40 inches in the northern part to actual desert conditions in Bechuanaland and southwestern Africa. The rains come largely during the summer months (winter in the Northern Hemisphere), and in this period they are fairly adequate except in the desert regions of Bechuanaland and along the West Coast. Temperatures are rather high except in a very limited mountain section in eastern South Africa. Plants that have developed under these conditions in Africa are well adapted to the Cotton Belt of the United States. Practically all of our cultivated varieties of sorghum originated in this region, and from there came Rhodes grass, Natal grass, and woolly fingergrass. Many species of *Chloris*, *Cynodon*, *Digitaria*, *Ehrharta*, *Hyparrhenia*, and *Themeda* contribute forage for their domestic and wild animals. Grasses that are abundant but of little value include the *Aristida* and *Trichopteryx* species, especially the latter.

Region 11 comprises most of Brazil, eastern Bolivia, Paraguay, Uruguay, and the northeastern part of Argentina. In this part of South America the rainfall is heavy (30 to 70 inches) and the temperatures are subtropical to tropical. Here we find an immense area of open parklike grasslands, including the campos of Brazil and the pampas of Uruguay and Argentina. The basin of the Amazon, with a rainfall of over 80 inches annually, is a dense, junglelike forest of little importance from a grass standpoint. Notwithstanding the extent of the grasslands in South America, few if any of the native grasses have shown any forage value in the United States or in their homeland. The superior forage grasses of South America were almost without exception introduced from tropical Africa, the native pampas grass being used chiefly as an ornamental because it is unpalatable. The molasses, jaragua, Guinea, and Para grasses all appear to have been introduced many years ago and are now widely distributed in region 11. They provide a large proportion of the pasturage for livestock, which is one of the main sources of revenue in this region.

Region 12 comprises Chile and the western or Andean sections of Argentina, Bolivia, and Peru as far north as the Gulf of Guayaquil. Except for southern Chile and Patagonia, this is a region of high altitudes and low rainfall. Although important as the native land of the potato and other Solanaceae, it does not appear promising as a source of forage grasses. *Axonopus scoparius*, a relative of carpet grass called "cachi" in Bolivia, is said to be a good pasture grass. This is found on the moist meadows of the eastern slope of the Andes. The forage in the high mountain valleys and plateaus is derived mostly from species of *Festuca*, *Poa*, *Calamagrostis*, and *Muhlenbergia*. Grasses that are abundant but have little agricultural value comprise numerous species of *Eragrostis*, *Stipa*, *Trisetum*, and *Piptochaetium*. The last-named genus is said to be encountered everywhere in this region, although it is uncommon in other parts of the world.

Region 13 includes southern Mexico, all of Central America and the West Indies, and Colombia, Venezuela, and Guiana in South America. This region, surrounding the Caribbean Sea and the Gulf of Mexico, is largely in the Tropics, but differences in altitude give it an extremely varied climate. It is also the home of the early Mayan civilization and the source of several of our most important food plants, including corn. In the Orinoco Basin of South America are the llanos, broad savannas or grasslands similar to the campos of Brazil. Several very useful forage grasses have been obtained from region 13, where they appear to be indigenous. The best known of these are teosinte, gamagrass, Bahia grass, St. Augustine grass, Guatemala grass, carpet grass, and wildrice. This region also abounds in species of *Trisetum*, *Setaria*, and *Andropogon*, most of which are of little or no value agriculturally. Sourgrass (*Trichachne insularis*) is very common but worthless.

Region 14 in western North America comprises a broad expanse of rugged mountains, dry plains, and plateaus extending from the Peace River section of Canada to southern Mexico. In all this region the rainfall is very limited, varying from actual desert conditions to 20 inches annually, while the temperatures range from very hot in Mexico and Arizona to very cold in northern United States and

Canada. The flora is rich in native grasses except for the desert areas, where the dominant vegetation consists of woody shrubs and cacti. Among the native grasses that contribute most to the sustenance of livestock are a great variety of wheatgrasses, bluestems or beardgrass, gramas, buffalo grass, sandgrass (*Calamovilfa* sp.), wildryes, fescues, bluegrasses, mesquite grasses (*Hilaria* sp.), and the Sacaton or dropseed grasses. Grasses that are common but of no particular value include the needlegrass (*Aristida* sp.), spear grass (*Stipa* sp.), and squirreltail grasses (*Sitanion* spp.). Foreign grasses that have proved adapted in this region include crested wheatgrass, awnless bromegrass, bulbous bluegrass, and Sudan grass.

Region 15, consisting of southeastern Canada and the northeastern United States, was originally occupied almost exclusively by hardwood and coniferous forests. Naturally, valuable native grasses are scarce except in the western part of the Corn Belt, which was from early days an open prairie carpeted with big bluestem and little bluestem. Both of these are excellent forage grasses. The rainfall in this region is usually adequate, and as the country was settled by people from Europe, the land when cleared of timber was seeded to introduced grasses from region 1. At the present time most of the pastures and meadows are occupied by these European grasses, which have proved admirably adapted to the climatic conditions here. Foxtail millet and Japanese millet, introduced from Europe but natives of Asia, are also grown rather extensively. Reed canary grass, big bluestem and little bluestem are about the only native grasses that have proved important. Other native grasses of minor importance are noted in table 1, because they may be of some value from a breeding standpoint.

Region 16 is that part of the Eastern United States south of the 60° isotherm. This is the original Cotton Belt, and while limited in area, it has been set apart from region 15 because of its marked difference in grass flora. This region was also originally a forest, and when the timber was cleared off by settlers European grasses proved unadapted, but more tropical grasses from Asia, Africa, and Central America have occupied the cleared lands where the soil is sufficiently fertile for these introduced grasses to compete with the omnipresent native broomsedge and other Andropogons. The most important of the introduced grasses are Bermuda, carpet, Dallis, and Johnson grasses, and they provide the bulk of the pasturage and hay in the region. Napiergrass, Japanese cane, and pearl millet also thrive here, but will not be discussed further at this time, since the situation in regard to grasses in the United States is presented in the appended detailed maps. The native grasses, some of which may offer possibilities in breeding, are listed in table 1. Texas bluegrass is one of these already used in crosses with Kentucky bluegrass.

CLIMATIC ADAPTATION OF PRINCIPAL FORAGE GRASSES OF THE UNITED STATES

The effective improvement of grasses by breeding requires an understanding of their inherent climatic relationships. In the United States this relationship is best expressed by dividing the country into six

regions as illustrated in figure 2. This generalized picture of a situation that has developed naturally under the influence of prevailing climatic factors provides a basis for the organization of grass breeding in this country. The introduction of other foreign grasses in the future may conceivably change the situation, especially in the Southwest. At this time, however, the opportunities for success in breeding appear to lie in working with those grasses that have met the require-

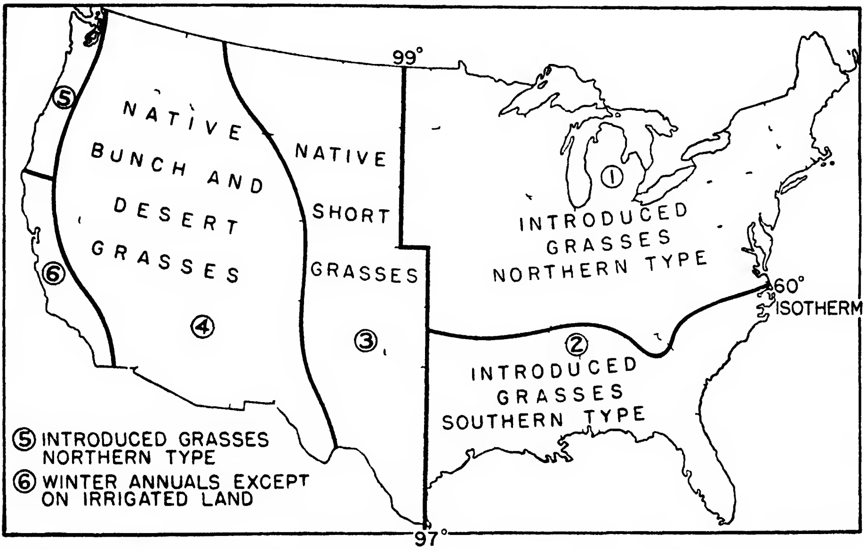

Figure 2.—Grasslands of the United States, showing the dominant type of grasses in each as determined by the climate.

ments of man and have been most productive during the past century. The most outstanding of these are discussed briefly.

In considering the distribution maps it must be understood that the limits indicated are not exact. Beyond the boundaries where a particular grass is really important it will be found less and less frequently struggling to survive under increasingly unfavorable conditions which results in an overlapping of adjacent distribution areas.

Kentucky Bluegrass, Canada Bluegrass, and Timothy

Kentucky bluegrass, Canada bluegrass, and timothy were introduced from Europe by the early settlers, and as the land was cleared of forest they spread over practically all of the humid part of the United States north of the 60° isotherm, as indicated in figure 3. In addition to the areas shown, these grasses are abundant in region 5 of figure 2, which is also humid. None of them is sufficiently drought-resistant to be grown successfully in arid or semiarid sections except under irrigation. These grasses have become the leading hay and pasture grasses of the United States and the adjacent sections of Canada. They proved so well adapted to climatic conditions here

that they now occupy much more extensive areas in North America than they do in Europe.

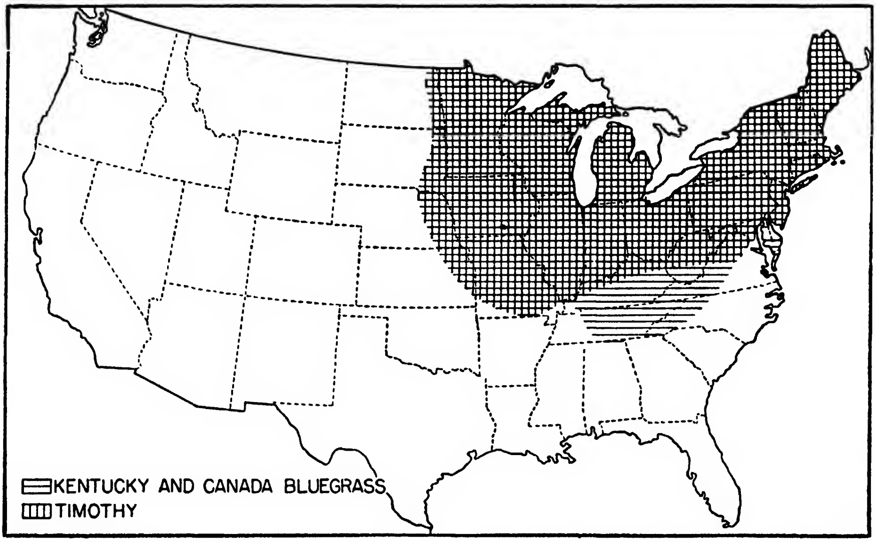

Figure 3.—Sections of the United States where Kentucky bluegrass and Canada bluegrass are well adapted and of primary importance.

Redtop and the Bentgrasses

Although redtop and the bentgrasses (species of *Agrostis*) are not so important agriculturally as are Kentucky bluegrass and timothy, redtop is valuable for both hay and pasture on wet or acid soils, and

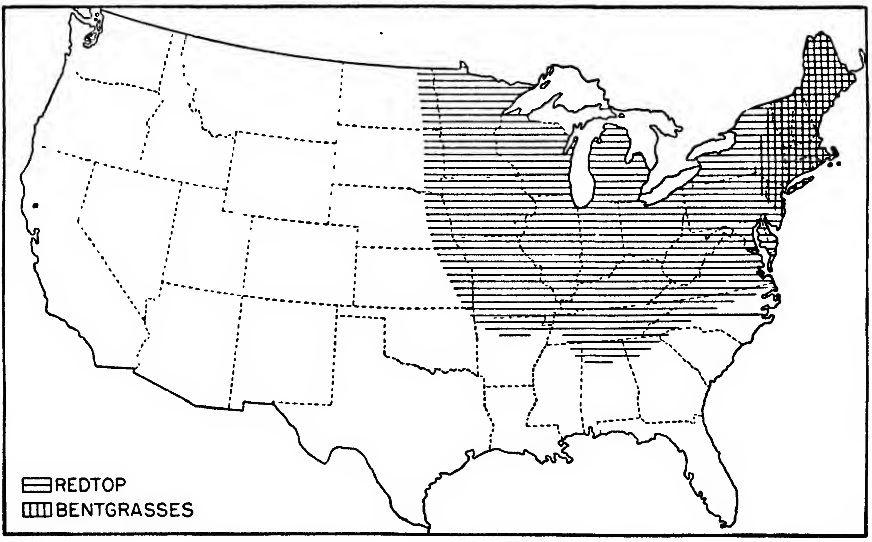

Figure 4.—Sections of the United States where redtop and the bentgrasses are well adapted and of primary importance.

the bentgrasses, because of their fine turf, are used extensively on lawns and golf courses. The sections where these grasses are of major importance are shown in figure 4, but they thrive equally as well in region 5 of figure 2, and the use of the bentgrasses for fine turf is common throughout the whole redtop region. Redtop is most highly regarded in Illinois, where most of the seed is produced. It seems better suited to the poorly drained, rather unproductive clay soils of that section than any other grass.

Orchard Grass and Tall Oatgrass

The approximate range of distribution of orchard grass and tall oatgrass is shown in figure 5. Of these two introduced grasses, orchard grass is the more common and undoubtedly the more valu-

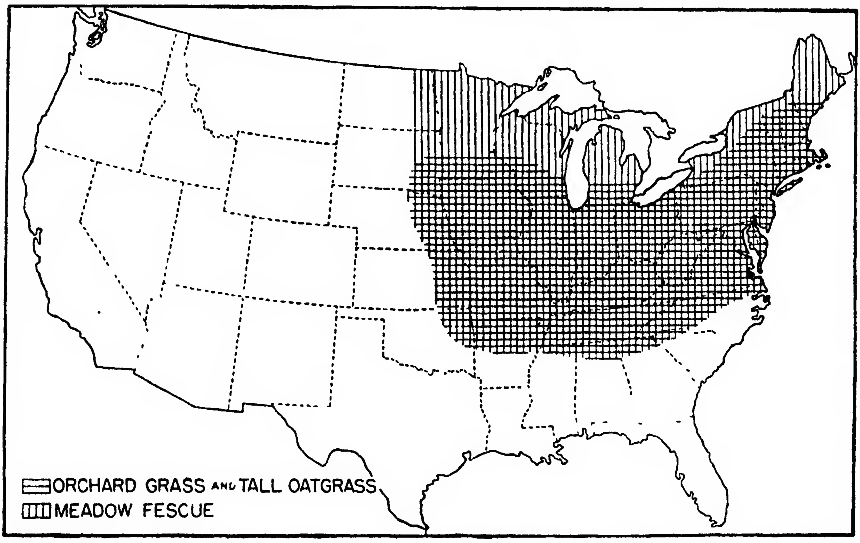

Figure 5.—Sections of the United States where orchard grass and tall oatgrass are well adapted and of primary importance.

able because of its longevity and its value in pasture mixtures. It is more tolerant of shade than bluegrass and produces better on poor soils. The results obtained in the improvement of orchard grass in Europe and Australia lead to the belief that much may be accomplished with it here. One of the obvious points of weakness in tall oatgrass is seed shattering which has already been overcome by selective breeding.

Bermuda, Johnson, and Dallis Grasses

Bermuda, Johnson, and Dallis grasses together with carpet grass are the principal hay and pasture grasses of the Cotton Belt. All of them were introduced at a comparatively early date and have spread naturally over most of these States. Although Bermuda grass and Johnson grass are found more or less frequently north of the limits indicated in figure 6, they are sensitive to low temperatures and grow

only during the frost-free period; hence they are unimportant outside of the section indicated in figure 6 except in the irrigated sections of southern California, Arizona, and New Mexico. In these States both are abundant, but Johnson grass especially is considered a weed and Bermuda grass is a doubtful asset. Both grasses invade irrigated

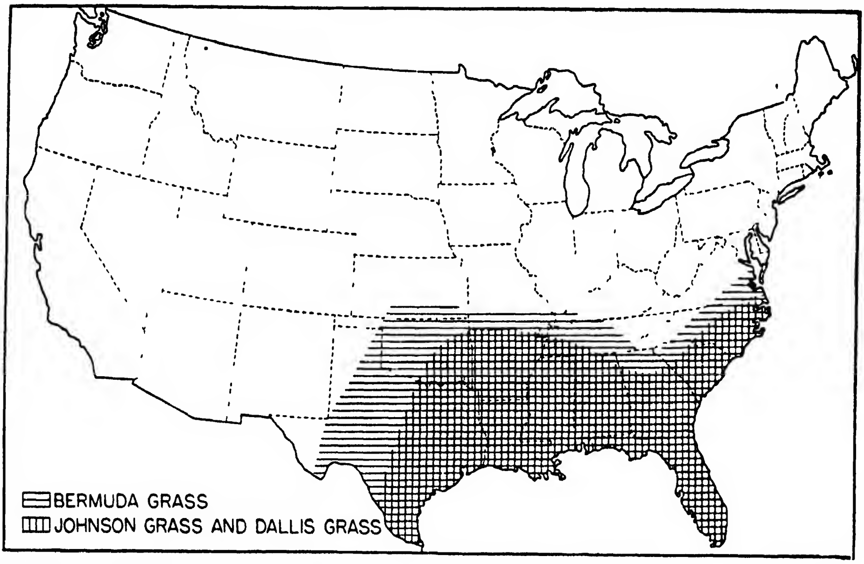

Figure 6.—Sections of the United States where Bermuda, Johnson, and Dallis grasses are well adapted and of primary importance.

cultivated lands and are difficult to control because of their aggressiveness. Dallis grass, however, is gradually coming to be recognized as a valuable constituent of pasture mixtures on irrigated lands in these States.

Carpet, Napier, Bahia, and Para Grasses

Successively more tropical and less winter-hardy, carpet, Napier, Bahia, and Para grasses are confined almost entirely to sections of the United States indicated in figure 7 and to extreme southern parts of California and Arizona. Carpet grass is much more common than the other three and next to Bermuda grass is foremost in pasture improvement. Napier grass, because of its large, coarse growth, may be used effectively as a soiling or silage crop in addition to its value as a supplemental pasture.

Awnless Bromegrass and Crested Wheatgrass

Awnless bromegrass and crested wheatgrass, unlike the grasses just discussed, are extremely winter-hardy, and both are very drought-resistant. Both were introduced from Europe and have been found most useful in the northern parts of the Great Plains and of the intermountain region (fig. 8). Bromegrass, however, is proving valuable

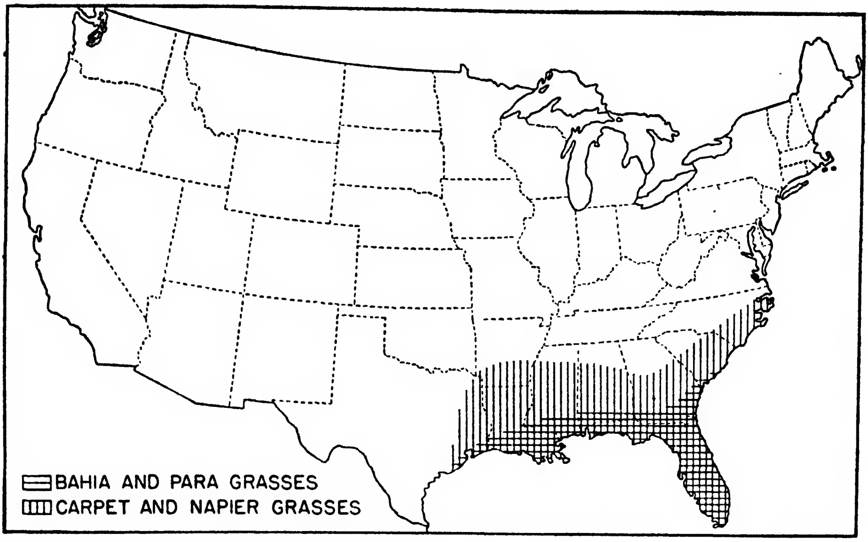

Figure 7.—Sections of the United States where carpet, Napier, Bahia, and Para grasses are well adapted and of primary importance.

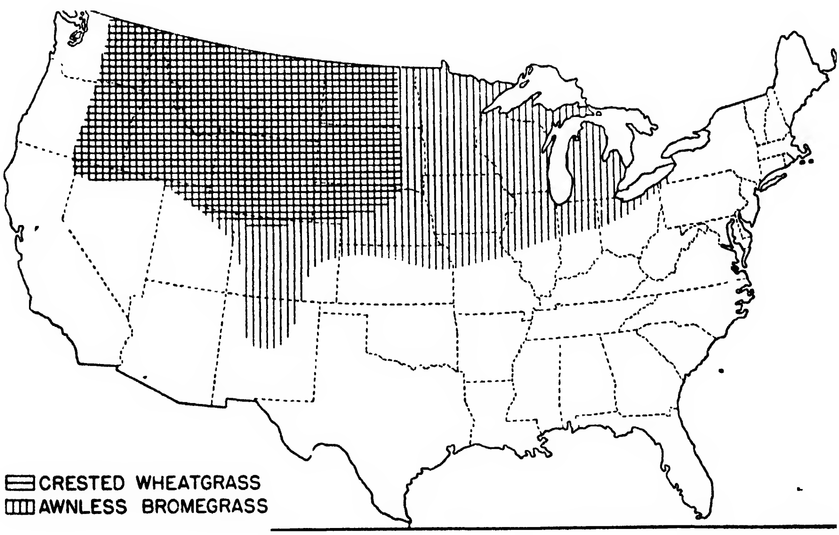

Figure 8.—Sections of the United States where awnless bromegrass and crested wheatgrass are well adapted and of primary importance.

in the North Central States in pastures and meadows, especially in mixtures with alfalfa. The chief objection to it, the difficulty encountered in eradicating it, may be overcome by selective breeding. Grazing animals are very fond of both crested wheatgrass and bromegrass.

Native Short Grasses and Prairie Grasses

Buffalo grass, the gramas, mesquite grasses, bluestems, and wheatgrasses supply a very large part of the pasturage and wild hay produced in the Great Plains. The distribution areas of all of these except the wheatgrasses are indicated in figure 9. Much of this region is semiarid, and in order to grow successfully here grasses must be able to endure periods of severe drought. All of these with the exception of big bluestem are preeminently drought-resistant, and the chief object in breeding will be improvement in productiveness of

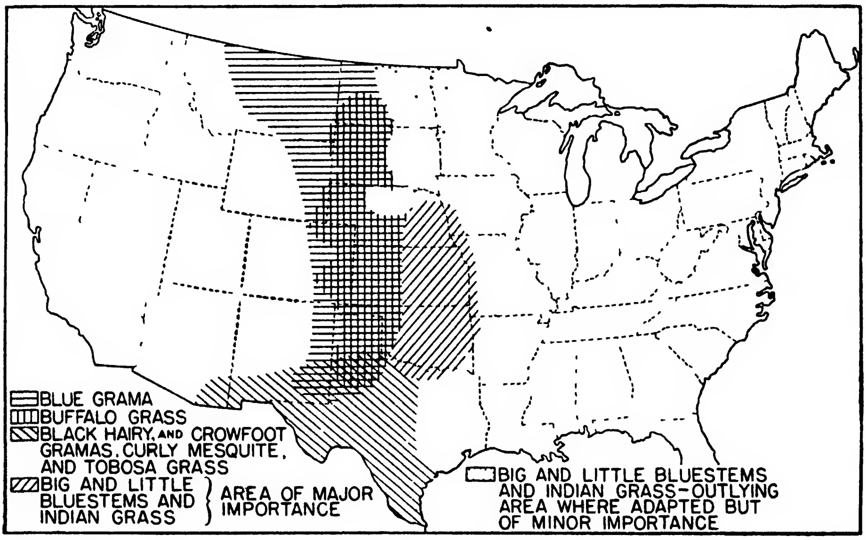

Figure 9.—Sections of the United States where native short grasses and prairie grasses are well adapted and of primary importance.

forage and viable seed. The actual distribution of each grass is considerably wider than is indicated on the map, which outlines the areas where each grass is of major importance and where their breeding is warranted. Big bluestem and little bluestem are adapted quite well to the outlying stippled area but are of minor importance there because most of the land is now under cultivation and introduced grasses are more productive. These two bluestems are found in small isolated colonies as far south as the Gulf coast. Indian grass is found growing in combination with the bluestems but rarely constitutes over 5 percent of the herbage.

Slender and Western Wheatgrasses

Western wheatgrass is found growing naturally all over the Great Plains except the extreme southern part. In the depressions where the soil is heavier, western wheatgrass often occupies the land to the virtual exclusion of all other grasses. Its foliage is rather harsh but palatable and very nutritious especially when immature. Slender wheatgrass is more widely distributed than western wheatgrass, although it does not extend so far south in the Great Plains as the

latter, and being a bunch grass it seldom occupies any large area to the exclusion of other grasses. The regions where these two native grasses are of importance are outlined in figure 10. Both are valuable for

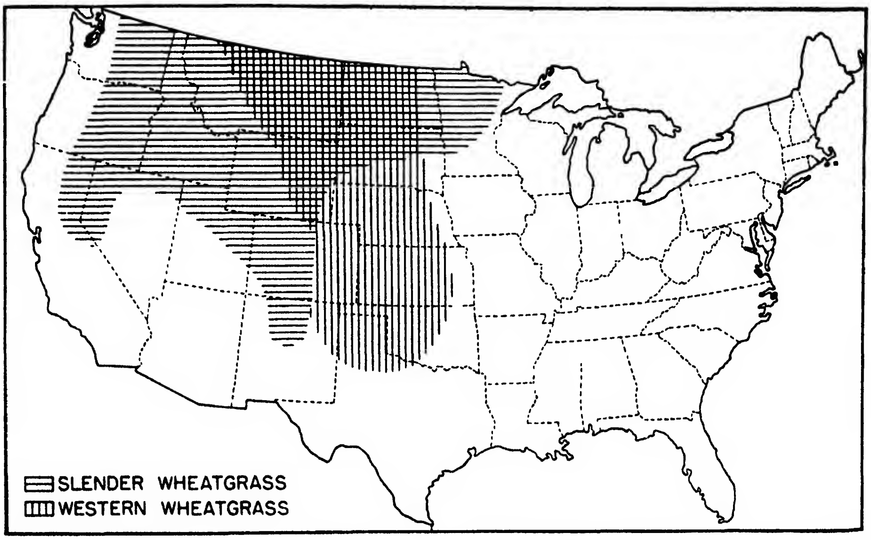

Figure 10.—Sections of the United States where slender wheatgrass and western wheatgrass are well adapted and of primary importance.

hay as well as pasturage, and less difficulty is found in obtaining viable seed of these wheatgrasses than of the other native grasses just discussed.

Sudan, Reed Canary, and Other Grasses

The species that have been discussed include nearly all of the grasses of recognized importance in the United States except Sudan grass and reed canary grass. Sudan grass, an annual, has been found useful as an emergency hay crop and for summer pasture in all parts of the United States, although best suited to conditions in the middle and southern Great Plains. Reed canary grass is valuable on wet lands anywhere north of the 60° isotherm. Breeding activities will no doubt be most productive with these grasses, but there are many others that should not be ignored, since in them are found useful characters that may be transferred to the more important species by hybridization.

WHY THE BREEDING OF GRASS IS WORTH WHILE

Approximately 60 percent (*32*) [4] [5] of the total land area of the United States is grazed at least part of the year, and a major portion of the feed obtained by grazing animals is provided by grasses. It is estimated that in 1919 the grazing lands supplied about 49 percent (*25*) and in 1929 about 41 percent (*33*) of the total feed consumed by all

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[4] Italic numbers in parentheses refer to Literature Cited, p. 1074.

[5] Acreage of pasture on farms is given for 1934. The National Resources Board also furnished data on grazing land (*33*, *pt. 2*, *table 2*, *p. 109*). The 1930 acreage figures for grazing land not in farms were adjusted by O. E. Baker for 1934.

classes of farm animals. If the 11,798,065 tons of hay from grasses other than timothy be included, approximately 43 percent of the sustenance of our farm livestock must be credited to miscellaneous grasses.

In addition to the farm animals there are in the United States over 1 million herbivorous game animals (*31*), including deer, elk, and antelope. Deer and elk are the most numerous, and they subsist largely by browsing on trees and woody shrubs, but 10 to 15 percent of the food of this group consists of grasses.[6] The grasses are also important in providing food and cover for wild fowl.

Results obtained by soil erosion experiment stations [7] indicate that on various soil types on slopes varying from 4 to 16 percent the losses of soil by erosion are from 650 to 4,600 times greater where the land is devoted to clean-cultivated crops as corn and cotton than on lands with a perennial-grass cover. Besides the reduction of direct losses through soil erosion and run-off, there is an additional benefit derived from a grass cover in the conservation of soil fertility, chiefly nitrogen and organic matter. It has been estimated that there is an average annual loss of 60 pounds of nitrogen per acre from cultivated soils. Hopkins (*8, p. 559*), of Illinois, found 4,000 pounds of nitrogen per acre in the surface soil of land that had grown corn for 16 years, as compared with 4,914 pounds per acre in the soil of adjoining pasture land. A determination of organic matter by the combustion method showed in the soil of old pastures 6.12 percent, new pastures 4.16 percent, and cultivated soil 2.44 percent (*37*).

Grass in lawns is the foundation of all landscape effects for private houses and public buildings. It has been estimated that over $100,000,000 is spent annually in the United States on private lawns and at least $10,000,000 for turf establishment and maintenance in cemeteries. To this must be added about $65,000,000 spent annually in providing the required turf on golf courses, athletic fields, and playgrounds, and $16,000,000 in providing a ground cover on airports, road shoulders, and railway embankments.[8]

An increase in the acreage of grasses and legumes has been definitely adopted as a national policy because grasslands not only conserve the soil but also contribute to a better balanced agriculture. This places a larger emphasis on the work of the breeder.

POSSIBILITIES AND PROBLEMS IN BREEDING GRASSES

In the United States breeding of grasses has received little attention with the exception of timothy. Orchard grass, bluegrass, redtop, bromegrass, bentgrass, Bermuda grass, carpet grass, and all other grasses ordinarily used in seeding pastures and lawns are mixed populations consisting of many strains varying in such important characteristics as date of maturity, disease resistance, leafiness (fig. 11), number, and vigor of the stolons and rhizomes, and viability and abundance of the seed—to name only a few of the many variations. There is,

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[6] U. S. Dept. of Agr., Bureau of Biological Survey. Wild Life Review. 1936. [Mimeographed.]

[7] The data are taken from unpublished reports or summaries of results from the various stations indicated: Guthrie, Okla., Soil Conservation Service Circ. L–1121 (1936); Temple, Tex., Soil Conservation Service Circ. L–1134 (1936); Hays, Kans., Soil Conservation Service Circ. L–1134 (1936); La Crosse, Wis., Soil Conservation Service Circ. L–1122 (1936).

[8] These estimates of expenditures were supplied by John Monteith, Jr., collaborator, Division of Forage Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.

therefore, a great opportunity for improvement by simple selection processes. The uses made of these grasses are varied as compared with those of cotton, tobacco, sugarcane, or even corn. This broad field of usefulness increases the opportunity, but it also implies a closer scrutiny and more thorough examination of the variants because a strain that may be of no value for hay purposes might be exactly the kind needed for pastures or lawns.

It is now rather generally acknowledged that the maximum values in plant breeding are attained only by breeding plants adapted to local conditions. Improved strains are not ordinarily found superior under

Figure 11.—Two selected strains of Kentucky bluegrass, showing the variations in leaf width found in individual plants of commercial cultures.

all conditions of soil and climate. There is therefore little reason to believe that the improved strains of grasses developed by British or other foreign workers will represent the best attainable here in the United States. Plant-breeding work with cereals has shown also that there are different strains of certain disease organisms, such as smut, and that a grain variety that is almost wholly immune to the ordinary smut may be susceptible to other strains of this disease. The same condition will probably prevail with reference to the diseases of forage grasses, which implies additional restrictions and necessitates better controlled tests in breeding.

Opportunities for the accomplishment of practical results in the improvement of forage and fine turf grasses appear most promising in the following respects:

1. Yield and viability of seed.
2. Disease resistance.
3. Ability to compete successfully with other plants.
4. Increased vigor and ability to renew growth quickly after defoliation.
5. Longevity, drought resistance, and winter hardiness.
6. Tolerance to wet or saline soils.
7. Palatability and nutritive value of herbage.
8. Quality, durability, and uniformity of texture in turf.

Increasing Yield and Viability of Grass Seed

Many valuable grasses are notably shy seed producers. This is especially true of our native grasses, but it also applies to many of the introduced grasses. The failure to produce viable seed in sufficient quantity to supply the demand is a great handicap and often prevents an otherwise valuable grass from being grown on an extensive scale; it prohibits a wide use of native grasses in regrassing abandoned farm land in the Western States; for example, the gramas, buffalo grass, big bluestem and little bluestem, wheatgrass, and several other species would be seeded on millions of acres of these lands if good, germinable seed were available in commercial quantities. The same thing is true of many of the promising introduced grasses. Woolly fingergrass from South Africa gives indication of being an outstanding pasture grass for the poor upland soil of the Southeastern States, but it produces little or no seed. The Japanese lawngrass (*Zoysia japonica*) appears to be exactly the kind of grass needed for sodding airports and athletic fields. It forms a tough, long-lived turf, which would endure rough usage and be more or less permanent. Here again seed production is negligible. Good seed of Dallis grass, Bahia grass, and centipede grass is scarce, and the use of these valuable pasture and lawngrasses is therefore limited.

Production of Disease-Resistant Strains

While diseases are not usually so destructive to the forage grasses as the rusts and smuts of cereal crops, there are several that present a definite handicap to the effective use of these grasses in certain localities. Sudan grass, immensely valuable in dry regions, is almost worthless in the humid portion of the United States from Washington, D. C., south to Florida, because of the ravages of foliage diseases. Ergot is the chief factor limiting the production of Dallis grass seed. A leaf-spot disease causes widespread damage to Kentucky bluegrass in pastures and lawns. Grass diseases are most feared, however, in the growing of fine turf on golf courses and lawns. Under certain conditions diseases like brown patch are the greatest menace to the fine turf grasses, especially bentgrass as it is grown and handled on the putting greens of golf courses and on lawns. Control of diseases of fine turf is possible through the application of fungicides, but the development of resistant strains or varieties is preferable. In the case of pasture and meadow grasses, the use of fungicides is not practical, and breeding for disease resistance is the only logical means of overcoming the difficulty.

Regulating Aggressiveness by Breeding

Most of our cultivated cash crops are grown in pure stands and occupy the land for only 1 year. Aggressiveness or ability to compete with weeds and other plants is not, therefore, a factor of any importance in these crops. With perennial grasses, however, the ability to retain possession of the soil to the exclusion of weeds and less desirable grasses is a characteristic of major importance in permanent pastures. In breeding grasses aggressiveness is a character that must be regulated. If it is too pronounced the grass becomes difficult to eradicate;

this is true of quackgrass and Bermuda grass. Another disadvantage of pronounced aggressiveness is the difficulty of growing legumes in combination with such grasses. In pastures and hay meadows also, a mixture of grasses and legumes is desirable not only because of the higher nutritive value of the mixtures but also from the standpoint of benefiting the soil. Carpet grass and centipede grass under favorable soil and climatic conditions produce so close a turf as to drive out all the clovers and lespedezas that may have been seeded with them. Bromegrass in the Dakotas and southern Canada has been condemned by some because of its tendency to become sod-bound and because it reappears in a field that has been plowed for the production of a cash crop. Thus in some cases breeding methods must be used to reduce aggressiveness and in others to increase it.

Increased Vigor and Quick Renewal of Growth After Defoliation

The ability to renew growth quickly after defoliation is important. Grasses are of low value in pastures or on ranges unless they are able within a reasonable time to replace by new growth the herbage removed by the grazing animal. Our best hay plants, such as alfalfa, are high producers because, after cutting and removing one crop of hay, new shoots appear immediately and grow as rapidly as the original stems, thus providing from two to eight cuttings a year. Among the grasses Sudan grass is a conspicuous example of a hay and pasture plant that comes back quickly after being cut or grazed. The extent and rapidity of growth in all plants is of course limited by soil and climatic conditions. Without a productive soil and adequate moisture supply either through rains or irrigation, continued luxuriant growth throughout the growth season is impossible. Fundamental differences however occur in the growth habits of plants that determine their behavior when clipped or grazed. Grasses that do not continually produce new growing points low down near the surface or underneath the surface of the soil are useless for lawns or golf courses because the turf becomes stubbly after it is clipped a few times. Hay plants that do not have a succession of buds at the crown capable of producing new shoots seldom produce more than one hay crop each season. The variation in these essential growth habits within a single species is marked and presents a good opportunity for improvement by selection processes.

Persistence or Longevity Fundamental in Pasture Grasses

Longevity under grazing conditions may be less important in the future than it has been in the past because of the present tendency to appreciate and demand high production in pastures. However, there will always be a large percentage of livestock producers who are willing to accept mediocre production from pastures and ranges in return for the assurance that this production level will continue indefinitely and reseeding will not be necessary. In some localities, like the semiarid regions, where the establishment of a satisfactory grass cover is difficult or highly uncertain, permanency may be the controlling factor in choosing a grass. Several factors such as drought resistance and

winter hardiness have an important bearing on the longevity of a grass. In breeding, therefore, longevity must be considered as a complex of several factors rather than a single one.

Drought resistance in plants has been the subject of much study in the arid and semiarid regions. It is not due to a simple Mendelian factor inherited as a unit character. Breeding for increased drought resistance will require a thorough understanding of the elements in plant composition and structure that enable certain plants to persist and produce better than others under low rainfall conditions.

Tolerance to Wet or Saline Soils

In the United States considerable areas of wet lands occur. Some of these overflow at more or less regular intervals; other areas have a high water table or are continually saturated by the seepage of drainage water from the land above them. In irrigated areas benchland ditches often produce seepage areas in the bottom lands below them, and such areas are frequently both wet and saline (alkaline). Poorly drained lands in arid sections are almost invariably unproductive because salts accumulate in the surface layer through evaporation.

Certain species of grass are known to be adapted to wet soils, and other species are especially tolerant of soil salinity. In both cases, however, these grasses are usually of low palatability and often of low nutritive value. A very real need undoubtedly exists for improvement of these grasses in palatability and nutritive value as well as for the development of strains with increased tolerance for the abnormal quantity of water or salts that such soils contain.

Increasing Palatability or Nutritive Value Difficult

Grasses adequate as forage for farm animals must be both palatable and nutritious. To increase either the palatability or nutritive value of a grass is perhaps the most difficult of all the breeding problems. The qualities that make a grass palatable are little understood, and the variations in nutritive value as indicated by chemical composition are slight within any one species. There is, therefore, little encouragement to attempt an improvement in these fields except by hybridization.

Quality, Durability, and Uniformity in Turf Grasses

Considerable success has already been achieved in selecting strains of bentgrasses that meet the special needs of the golfing public. For the putting greens of golf courses both fine texture and uniformity are required (fig. 12); otherwise the path of the putted ball will be uncertain. Disease resistance, longevity, and aggressiveness are factors of great importance on both golf courses and lawns in order that the turf may be permanent and free of weeds and weedy grasses.

On athletic fields and playgrounds, and especially on airports, durability is the first consideration. A satisfactory turf for such purposes must be able to withstand the tearing and gouging of cleated or spiked shoes and the terrific impact of the landing gear on airplanes. To do this the grass must be deep-rooted and tough and also able to cover quickly gashes made in this way with spreading stolons or rhizomes.

CURRENT BREEDING WORK, ITS OBJECTIVES AND RESULTS

Selective Breeding of Grasses in the United States and Canada

Replies to questionnaires on grass breeding submitted to various agricultural institutions reveal the fact that selection for improvement is under way with a large number of grasses other than timothy. Limited and more or less desultory activities in this field have been in progress for 16 years or more, but organized and intensive grass-breeding activities, for the most part, have been inaugurated within the last 5 years. The various grasses included in the current selective breeding programs of State and Federal institutions in the United States and Canada are listed in table 2. It is apparent that a considerable number of workers are now concerned in developing superior pasture and turf grasses. The results accomplished by selective breeding in foreign countries other than Canada are not discussed in

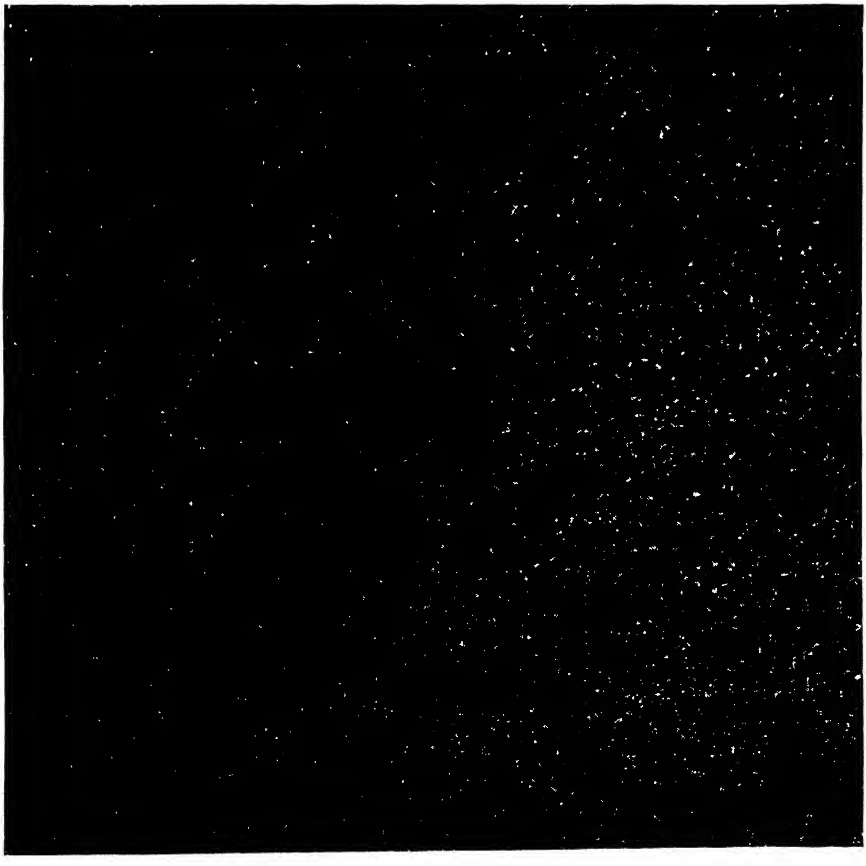

Figure 12.—A turf plot of Metropolitan bentgrass illustrating the fine texture and uniformity required for the putting greens of golf courses.

detail because of the limitations of space and the fragmentary information obtained in response to the questionnaires. We have also to consider the fact that very few of the improved strains of grasses developed in Europe, Australia, or New Zealand have shown outstanding value in the United States. In Canada, however, the species under investigation are the same as those in the United States

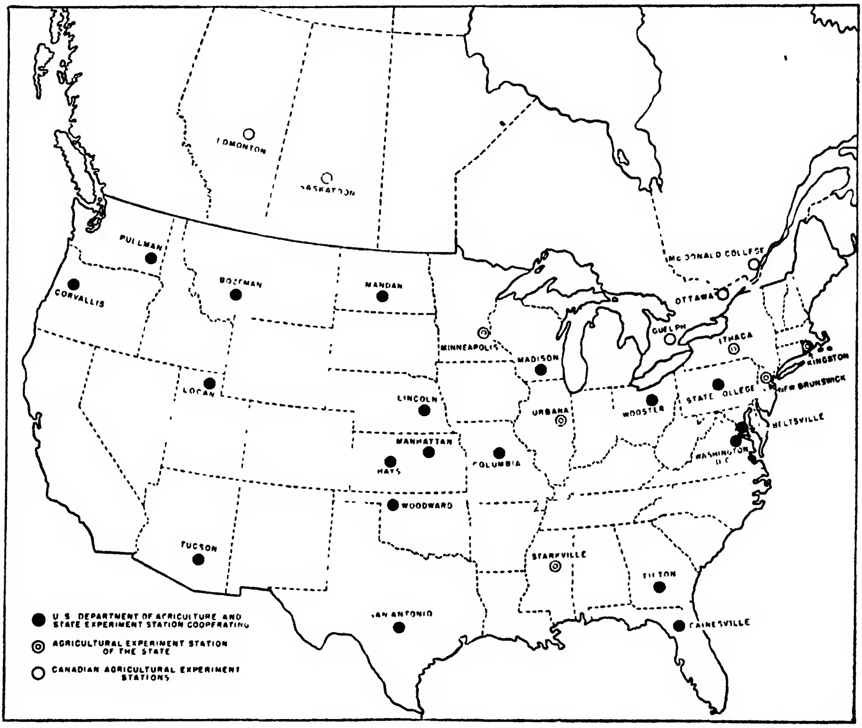

Figure 13.—Locations of experiment stations in the United States and Canada where organized grass-breeding work is in progress.

and climatic conditions are similar to those in our Northern States, hence results there should be helpful to our plant breeders. The locations of experiment stations in the United States and Canada where organized grass-breeding work is in progress are shown on the map in figure 13.

Improved or Elite Strains Developed by Selection

In the United States very few improved strains have yet been introduced into cultivation, but notable progress has been made, especially in the fine-turf grasses. The new strains already introduced, or soon to be ready for introduction, include:

Washington and Metropolitan bent grass: These two strains of creeping bent grass developed by the green section of the United States Golf Association have replaced other grasses on a large percentage of the putting greens of golf courses throughout the country.

The fact that these turf grasses, when used on putting greens, are usually propagated vegetatively makes it easy to keep the strains pure and preserve their identity.

Velvet bent grass, strain F. C. 14276: This has shown marked superiority over the ordinary strain of velvet bent grass in vigor, disease resistance, and quality of turf.

Promising turf strains of *Poa pratensis* and *P. trivialis* have also been developed by the green section of the United States Golf Association, but these are not yet ready for distribution.

H. A. Schoth, of the United States Department of Agriculture, cooperating with the Oregon Agricultural Experiment Station at Corvallis, Oreg., has several improved strains ready for distribution.

Highland Reed canary grass: This is definitely superior on upland soils; it is a heavy seed producer, and the seed shatters less freely than that of the ordinary strain. Seed of this improved strain is now being produced and marketed commercially.

Tall fescue, strain F. C. 29366: This has softer or less harsh leaves than the ordinary tall fescue and in general improved quality of foliage and better seeding habits. Seed production of this tall fescue will be on a commercial basis in 1937.

Tall oatgrass, strain F. C. 29367: The fault of seed-shattering characteristic of this species has been remedied almost completely. In this strain the seed increase is just in the initial stages, so that it is not ready for commercial distribution.

Bahia grass, strain F. C. 19774: A selection made in 1929 by F. H. Hull, associate agronomist, Florida Agricultural Experiment Station, Gainesville, Fla., on the basis of stigma color has proved definitely more resistant to the helminthosporium leaf disease than the ordinary strain. This selection has been compared with the common strains of Bahia grass by George E. Ritchey, of the United States Department of Agriculture, at the Florida station. Arrangements are being made to increase the seed of it in Arizona as a source of commercial seed production.

Tift Bermuda grass: A vigorous, fine-stemmed strain selected by J. L. Stephens, of the United States Department of Agriculture, at the Georgia Coastal Plain Experiment Station, Tifton, Ga. This strain is much more productive as a hay plant than the common Bermuda grass. In 1936, when 400 pounds per acre of complete fertilizer were applied, 2 tons per acre of fine quality hay were obtained in two cuttings. In the past it has been propagated vegetatively, since Bermuda grass does not produce viable seed in Georgia, at least in any quantity.

Reed canary grass, Iowa 503: This was selected by H. D. Hughes and F. D. Wilkins, agronomists at the Iowa Agricultural Experiment Station, from the progeny of seed sent to them by an Iowa farmer in 1918. The strain produces high yields of both hay and seed and appears valuable also in pastures because it makes a rather dense turf and remains green late in the fall. It was distributed to farmers in 1930 under the name Iowa Phalaris.

In Canada, where agricultural workers have devoted more attention to breeding problems, a considerable number of improved forage and

turf strains have been developed and are now in commercial production. Among those reported by Canadian workers are the following:

Grazier slender wheatgrass: A leafy uniform strain that produces a high yield of pasturage and hay. Developed by G. P. McRostie and L. E. Kirk at the Central Experimental Farm, Ottawa, Ontario.

L. E. Kirk, before his removal to Ottawa, and T. M. Stevenson, working at the Dominion Forage Crops Laboratory, Saskatoon, Saskatchewan, developed four elite strains or varieties, namely:

Figure 14.—O. McConkey, associate professor, Department of Field Husbandry, Ontario Agricultural College, Guelph, Ontario, Canada, who, with L. E. Kirk, of Ottawa, has pioneered in grass-breeding investigations in Canada.

Mecca slender wheatgrass: A high-yielding hay variety.

Fairway crested wheatgrass: A rather dwarf, fine-stemmed, leafy strain that usually produces lower yields of hay than ordinary crested wheatgrass but is superior to the latter for use on lawns and on the fairways of golf courses. Already the Fairway strain has a wide use in the western parts of the United States and Canada.

Superior bromegrass: This was developed by Kirk from material collected by J. Bracken prior to 1921. It is now definitely established as a high-yielding hay and pasture variety.

Parkland bromegrass: Characterized by a reduced rhizome development that makes it to all intents and purposes a noncreeping variety. Parkland bromegrass does not become sodbound so quickly as ordinary bromegrass and is less difficult to eradicate when grown in rotation with cultivated crops.

Fyra slender wheatgrass: This was developed by M. O. Malte and G. H. Cutter at the University of Alberta, Edmonton, Alberta, as an improved hay variety.

Avon orchard grass: Developed by workers in the Agronomy Department of MacDonald College at Quebec, this strain had its origin in foundation stock introduced by L. S. Klinck, 1911–14. Selfed lines were isolated by L. A. Waitzinger, G. P. McRostie, and A. MacTaggart in the period 1914–30, and J. N. Bird in subsequent years has combined the most promising of these genotypes to form the strain called Avon. The Avon is decidedly more winter-hardy and therefore longer lived and produces larger yields of hay and aftermath than commercial orchard grass. Increased seed production of the Avon is in progress at MacDonald College.

In addition to the named strains herein credited to Canadian breeders, O. McConkey (fig. 14) and his associates at the Ontario Agricultural College, Guelph, report (Y. B. Q.)[9] that 23 improved strains of grasses are being increased for more extended trials and distribution at Guelph. These include the species listed for Guelph in table 1.

[9] This abbreviation will be used in the following pages to indicate that the information was received in reply to the Yearbook questionnaire, sent out in the cooperative survey of plant and animal improvement.

Reservoirs of Plant Material for Selection

The most important sources of material for selection are, of course, the ranges, pastures, and meadows where grasses have been established for a good many years. From this primary source and from foreign lands the United States Department of Agriculture in cooperation with State experiment stations has brought together for

Figure 15.- Grass nursery maintained by the Bureau of Plant Industry and the Soil Conservation Service of the United States Department of Agriculture at the Northern Great Plains Field Station, Mandan, N. Dak. Side-oats grama in the middle foreground.

comparison in grass nurseries extensive collections of native and introduced species. Seed of all the more important native grasses was collected by the Soil Conservation Service in 1935 and 1936 throughout the arid and semiarid Western States. Seed or propagating material of foreign species has been obtained through the Division of Plant Exploration and Introduction of the Bureau of Plant Industry for many years, and these and the native species are available to plant breeders in nurseries (fig. 15) maintained at field stations of the United States Department of Agriculture and at State experiment stations and substations where cooperation with the United States Department of Agriculture exists. Such cooperation is indicated in table 1.

Selective Breeding in Foreign Countries Other Than Canada

Breeding work with grasses has been developed much more in the British Isles, New Zealand, Australia, Sweden, Germany, and Denmark than in the United States.

The Imperial Bureau of Plant Genetics, Aberystwyth, Wales, has made the greatest contribution in the work on herbage grasses, under the direction of R. G. Stapledon. The technique for producing and distributing improved strains of grasses that has been developed

by Stapledon and his associates, especially T. J. Jenkin (fig. 16), should be very helpful in formulating a program for similar work in the United States. It is described fully in a publication of that bureau (*11*).

The results achieved in the British Isles and New Zealand also provide proof of the practical value of a comprehensive grass-breeding program. Levy (*18*) agrostologist, New Zealand Department of Agriculture, reports progress in the use of improved strains of perennial ryegrass as follows: "The North Island is using over 95 percent certified (seed) and it is difficult to dispose of uncertified at any price."

Figure 16.—T. J. Jenkin, who is associated with R. G. Stapledon at the Welsh Plant Breeding Station and has made many important contributions to the science and art of grass breeding. He is responsible for the breeding of all grasses except orchard grass and for the development of a breeding technique.

While the work at the Welsh Plant Breeding Station and in New Zealand is perhaps most outstanding, excellent breeding work has long been under way at the Northumberland County Agricultural Experiment Station at Cockle Park near Newcastle, England; at the Scottish Plant Breeding Station near Edinburgh, Scotland, and in South Africa and Australia. F. Nilsson and A. Muntzing, of the Seed Control Station, Swedish Seed Association, Svalöf, Sweden; H. Weller, Weihenstephan near Munich, Germany; and H. N. Frandsen, Stoftegaard, Denmark, are also making valuable contributions in grass improvement and breeding technique.

The map in figure 17 gives the locations of foreign grass-breeding stations.

Progress in Hybridization of Grasses

Improvement by selection within a species or variety is usually the first step in a breeding program. In every crop, however, the plant breeder ultimately resorts to hybridization as a means of inducing greater variation and also in order to combine in one plant the desirable characters found in different species or genera of plants. The question of how soon hybridization should become a part of a breeding program is not an easy one to answer. Many believe crossing of species and genera should not be undertaken until the possibilities of improvement by selection have been virtually exhausted and approximately pure lines have been obtained for use as parents of the cross. Several potent reasons exist for earlier use of this effective method of plant improvement: (1) To wait until the possibilities of selection

are exhausted would delay hybridization benefits almost indefinitely; (2) strains developed by hybridization usually show more marked difference from the ordinary strain than do selections and are therefore easier to identify and keep pure in commercial trade channels; and

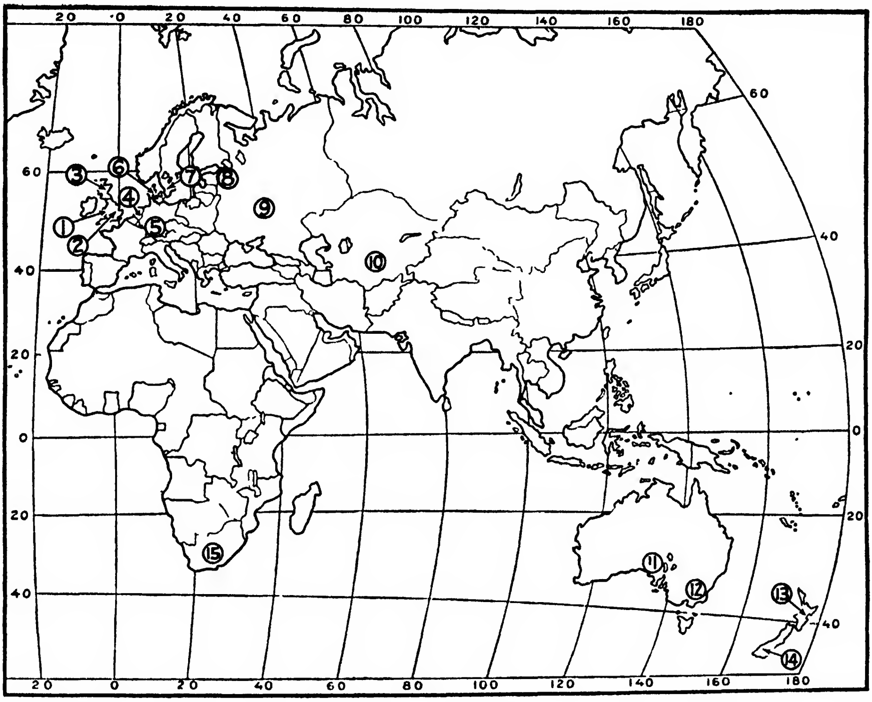

Figure 17.—Locations of the principal grass-breeding stations in the Eastern Hemisphere: 1, Welsh Plant Breeding Station, Aberystwyth, Wales; 2, Northumberland County Agricultural Experiment Station at Cockle Park, near Newcastle, England; 3, Scottish Plant Breeding Station, near Edinburgh, Scotland; 4, Rijksstation voor Plantenveredeling, Ghent, Belgium; 5, Landessaatzuchtanstalt, Weihenstephan, near Munich, Germany; 6, Danish Plant Breeding Station, Stoftegaard, Denmark; 7, Seed Control Station, Swedish Seed Association, Svalöf, Sweden; 8, Institute of Plant Industry, Leningrad, Union of Soviet Socialist Republics; 9, Institute for Fodder Crops, Moscow, Union of Soviet Socialist Republics; 10, Central Asia Scientific Research Institute of Plant Protection, Tashként, Union of Soviet Socialist Republics; 11, Waite Agricultural Research Institute, Adelaide, Australia; 12, Commonwealth Council for Scientific and Industrial Research, Canberra, Australia; 13, Plant Research Station, Department of Agriculture, Palmerston North, New Zealand; 14, Canterbury Agricultural College, Lincoln, Canterbury, New Zealand; 15, Prinshof Pasture Research Station, Pretoria, South Africa.

(3) the intelligent combining of desirable traits, such as disease-resistance, with good forage characters, is often possible by crossing.

Breeders have successfully crossed many species of grasses and in several instances have been able to combine closely allied genera. For the information of present and future workers in this field the hybrids between species are listed in table 3 and the hybrids between

genera in table 4 in the appendix. It will be noted that a large proportion of these hybrids are the products of foreign workers, Russian plant breeders having been especially active in this field. A number of the hybrids are combinations of the relatives of wheat and rye.

Figure 18.—*Triticum-Agropyron* hybrid produced by W. J. Sando, United States Department of Agriculture, showing the hybrid vigor attained in the first generation. From left to right, *Agropyron elongatum*, hybrid, *Triticum aestivum*.

Some of these, especially the *Triticum-Agropyron* hybrids, appear to have marked forage value (fig. 18). Sando, of the United States Department of Agriculture, and Armstrong, of the Canadian Department of Agriculture, who have had an opportunity to observe such hybrids, are convinced that many of the segregates of these crosses

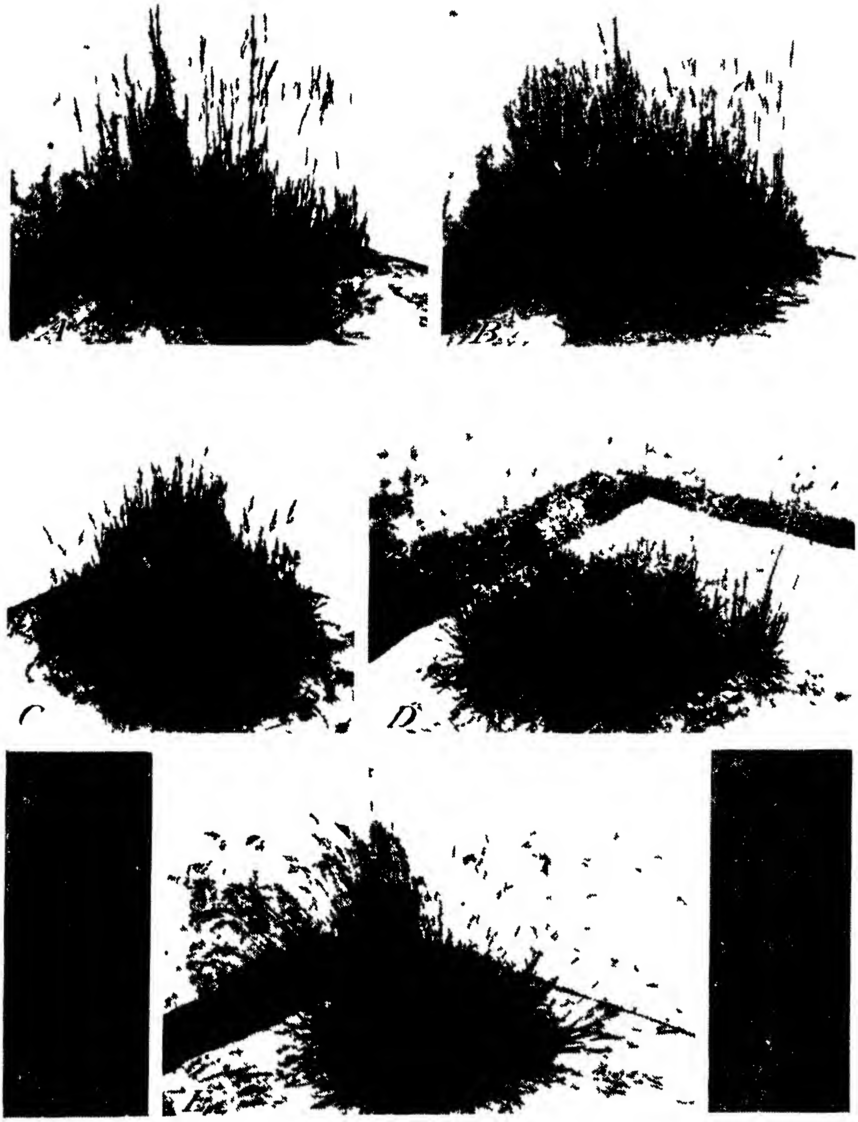

Figure 19.—A few of the variants found in the first-generation hybrid of a cross *Poa arachnifera* × *pratensis* *A*, Texas bluegrass type; *B*, *C*, and *D*, intermediate types, *C*, being one of the less desirable; *E*, Kentucky bluegrass type.

will have great value from a forage standpoint. Armstrong (*1*) states in his report: "Their [the Russian plant breeders] chief aim has been the creation of new forms of perennial wheat. For Canadian conditions the possibilities of obtaining new forms of forage crops by this method appear more attractive." Arrangements are now being made by the United States Department of Agriculture to study the forage value of Sando's crosses.

Jenkin, of the Welsh Plant Breeding Station, has successfully crossed the two genera *Festuca* and *Lolium* and has also made many hybrids among the species within these genera. Brief notes on the progeny characters of these hybrids will be found in tables 3 and 4. No new strain of superior value has resulted from these crosses to date, and Jenkin reports that more immediate improvement in forage

Figure 20.—Single plants representing the various types found in the first generation of a cross *Poa arachnifera* × *pratensis*. These plants were grown on the United States Department of Agriculture grounds in 1909 from seed of crosses made by George W. Oliver the previous year.

value can be attained through selection within a species than in the progeny of the crosses he has made.

This evidence of the futility of hybridization methods cannot be accepted as final, however. In many instances repeated backcrossing has been found necessary to produce the desired types. Muntzing, of the Swedish Seed Association, found in the progeny of a backcross (*Dactylis glomerata*×*aschersoniana*×*glomerata*) individuals more vigorous than *D. glomerata*. Texas bluegrass (*Poa arachnifera*) is dioecious, having the male and female spikelets on different plants. Using the pistillate plants as the female parent, E. Marion Brown, of the United States Department of Agriculture, made crosses of this species and Kentucky bluegrass at Columbia, Mo. He reports wide variation (fig. 19) in the first-generation plants, including individuals more resistant to heat and drought and more productive than Kentucky bluegrass. This cross was made first in 1908 by the late George W. Oliver. Oliver also found an unusual degree of variation (fig. 20) in the first-generation hybrid of this cross, but there was little interest in grass breeding at that time and nothing came of it. These results, in addition to the observed forage value of the *Triticum-Agropyron* hybrids, encourage further hybridization efforts.

GRASS GENETICS AND HYBRIDIZATION TECHNIQUE [10]

To ACHIEVE the utmost possible success in breeding within any group of crop plants, a thorough understanding of the genetics of the plant species is necessary. It is a fact that a large number of the improved varieties that find their way into commercial channels are produced by the selection of existing variants or by breeders who consciously combine the desirable qualities of several varieties or species by crossing or hybridizing them without having any definite knowledge of the manner in which the desired character is inherited. The genetic analysis of any species of plants or animals is extremely slow work, and many of the results obtained have no practical application. Individuals who accomplish most in the realm of pure genetics are not likely to be concerned overmuch as to whether new and improved crop varieties result directly from their research. Practical plant breeders are, however, impatient of delay and usually proceed without knowing quite what to expect in the progeny of a hybrid but fully convinced that something good will be found in the segregates if the parents of the cross have been intelligently chosen. With the grasses as with corn and wheat the more or less unscientific breeding operations have preceded the genetic investigation. Henceforth the two phases of breeding will no doubt progress to-

Figure 21.—*Phalaris truncata*, a foreign relative of the reed canary grass having a spikelike panicle. Note the progress of blooming from apex to base. Panicle on left began to bloom 2 days earlier than that on the right.

[10] The following section is intended primarily for students and others professionally interested in genetics or breeding.

gether. As specially trained groups of geneticists become interested in the study of forage grasses, the fund of basic information regarding their genetic constitution will increase rapidly. At present it is most inadequate. We do, however, have some knowledge of certain characteristics of our more important grasses that are useful in genetic studies. These will be discussed briefly.

Figure 22.—**Flowering panicle of Kentucky blue grass, illustrating the loose, open type of inflorescence found in many grasses.**

Flowering Habits of Grasses

The inflorescence or flower-bearing organ of grasses may be a compact spikelike panicle as in canary grass or a more or less loose panicle as in orchard grass or bluegrass (figs. 21 and 22). Regardless of the type of inflorescence, flowering begins near the apex of the inflorescence and progresses more or less regularly toward the base. In the spikelet the reverse is true; the basal florets open first, followed in regular order by those above. Through the courtesy of Mrs. Agnes Chase, of the Division of Plant Exploration and Introduction, Bureau of Plant Industry, the essential floral organs, the floral envelope, and the arrangement of florets in the spikelet are shown in figure 23.

Grasses flower, that is, extrude their stamens and liberate pollen, most abun-

dantly in the early morning. This is an almost universal rule (*3*), although the period of flowering may be delayed and prolonged by cloudy atmospheric conditions. For several grasses at least there is apparently a secondary, less intensive anthesis period in the afternoon. Fruwirth (*5*), who from 1906 to 1915 conducted some important and rather extensive studies of anthesis and pollination in grasses, reports a secondary blooming period in the afternoon that lasted only 1 or 2 hours. This work was conducted at Hohenheim and Waldhof, near Amstettin, Germany. Sando[11] found in *Agropyron elongatum* the maximum anthesis between 6 and 8 a. m., but there

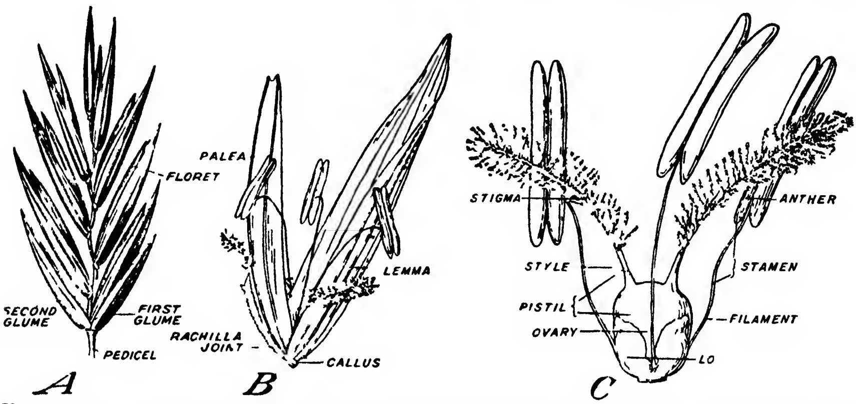

Figure 23.—A grass inflorescence is composed of spikelets, florets, and flowers: *A*, Generalized spikelet indicating the alternate arrangement of florets on the rachis and relative positions of the glumes; *B*, grass floret opened as at blooming time, showing how the lemma and palea are forced open by the lodicules; *C*, typical grass flower showing the essential floral organs necessary in fertilization.

was another period of activity between 3 and 4 p. m. "No blooming occurred between 8 a. m., and 3 p. m." Sando also reports that blooming is most active when the sun is shining and the temperature 70° F. or above. No blooming was ever observed at temperatures below 52°. He believes the delay or reduction in anthesis caused by a cloudy sky is due more to the lowering of temperatures than to increased humidity.

The views of Sando respecting the effect of humidity are confirmed by the studies of Stephens and Quinby (*29*) on sorghum (*Sorghum vulgare*). They concluded, "Relative humidity apparently did not influence the time of blooming." Since sorghum is a grass, it is interesting to note that under field conditions at Chillicothe, Tex., the rate of blooming in the sorghums was highest shortly after midnight rather than in the early morning as Sando found for his *Agropyron* and *Triticum* species growing in the greenhouse. Although the hour of maximum blooming activity in sorghum varied with varieties, Stephens and Quinby state, "A relatively small proportion of flowers opened before 10 p. m. or after 8 a. m., but there were no hours in which flowers were never found opening." By placing plants in a dark room during the day and exposing them to artificial light at

[11] Personal correspondence, 1936.

night the natural rhythm of blooming was reversed in 36 hours. It would appear, therefore, that light conditions are a most important factor in governing the time of blooming. They found, however, that lowering the temperature reduced the rate of blooming.

Fruwirth (*5*) agrees with Stephens and Quinby regarding the effect of humidity but not as to light. In an experiment with ryegrass and orchard grass in which he placed a box lined with black paper over the plants to exclude all light rays, he found that the plants bloomed in spite of the lack of light. He concluded from this experiment in which the heat was sufficient but light was lacking, that the latter seemed to be unnecessary for blooming. There is one criticism to be made of this experiment in that Fruwirth did not alternate darkness and light but left the box in place day and night. Recent investigations have emphasized the importance of the relative proportion of daylight and darkness in the reproduction processes of plant development.

Wolfe (*38*) in his studies of orchard grass at Blacksburg, Va., observed 76.9 percent of the flowers blooming from sunrise to noon, 6.6 percent from noon to sunset, and only 0.3 percent from sunset to midnight. The maximum blooming occurred from 8 to 9 a. m.

Jenkin (*9*) in 1921 observed for several grasses the time on "very fine days" when anthers were exserted under cool greenhouse conditions. These results show that the greater part of the blooming takes place in the forenoon. His recorded observations were as follows:

Lolium perenne.—Blooming period 9 a. m. to 11 a. m.; maximum 9:15 to 9:30 a. m.

Festuca rubra.—Blooming period 9:45 a. m. to 2:30 p. m.; maximum 12 to 1 p. m.

Alopecurus pratensis.—Blooming period 6 to 7:45 a. m.; maximum 6:30 to 7:30 a. m.

Phalaris arundinacea.—Blooming period 5 to 10:15 a. m.; maximum 6 to 6:30 a. m.

The author does not state in what month these observations were made. He does say, however, that in the open "these species apparently flower rather earlier while in dull weather in the greenhouse anther exsertion may be considerably delayed and * * * may be very poor for several days." Jenkin found that orchard grass, tall oatgrass, and timothy, unlike the perennial ryegrass and red fescue, begin blooming early in the morning.

Self-Fertility in Grasses and its Relation to Effect of Inbreeding

The fertility of many important grass species has been summarized in great detail by Beddows (*3*), of the Welsh Plant Breeding Station, who made a thorough review of the literature on this subject. He found that as a general rule the annual grasses were "highly self-fertile", but the perennials showed a high degree of self-sterility. Exceptions occurred however, in both cases, and in certain species there was a marked variation in respect to this character within the species. Nilsson (*21*), of Sweden, made a detailed study of fertility and the effect of inbreeding in meadow fescue, orchard grass, and timothy. As would be expected, the effect of close fertilization or

inbreeding varies in different species according to whether they are naturally cross-fertilized or self-fertilized. The situation regarding these characters as they affect a few of our more important grasses will be found useful in breeding by either selection or hybridization methods.

Orchard grass or cocksfoot (*Dactylis glomerata*): Stapledon (*27*) found *D. glomerata* normally setting much more seed when cross-fertilized than when self-fertilized, but containing "representative plants which are highly self-fertile." These results have been confirmed by breeders in the United States and Canada. Stapledon says, "There is every reason to suppose that completely self-fertile, single plant lines could be isolated." Regarding loss of vigor from inbreeding he concludes that on the average selfed plants are about half as vigorous as plants produced by crossing. He found, however, certain "robust" plants that showed little loss in vigor when selfed for five generations. There is, therefore, an opportunity to use inbreeding methods on this species to purify lines.

Perennial ryegrass (*Lolium perenne*): Jenkin (*10*) and Gregor (*7*) report a low degree of self-fertility in *L. perenne*, but great variation between plants in this respect. Some plants were completely male-sterile while others were comparatively self-fertile, so that Jenkin (*10*) concludes "breeding for self-fertility would not be a difficult matter" in perennial ryegrass. Beddows (*3*) reports 3.6 times as much seed produced in open-fertilized as in close-fertilized plants.

Loss of vegetative vigor resulting from continued inbreeding of unselected perennial ryegrass plants is extreme. Jenkin (*11*) reports an average loss of vigor approximating 63 percent when plants were selfed or fertilized with pollen from other plants of the same line. He concludes, "In perennial ryegrass loss of vigor from selfing is extreme, and consequently the results from other forms of inbreeding will also be relatively pronounced." Wenholz and Whittet, of Australia (Y. B. Q.), confirm Jenkin's results and have discontinued the practice (selfing) in breeding perennial ryegrass.

Italian ryegrass (*Lolium multiflorum*): The conditions regarding self-fertility and loss of vegetative vigor are about the same in Italian as in perennial ryegrass.

Crested wheatgrass (*Agropyron cristatum*): White (Y. B. Q.), of Saskatchewan, reports that sterility is very marked in caged or bagged plants, although this evidence of self-sterility is not conclusive. He found also a large decrease of vegetative vigor in close-fertilized plants, which indicates a low degree of self-fertility.

Slender wheatgrass (*Agropyron pauciflorum*): Malte (*19*), of the Central Experimental Farm, Ottawa, Ontario, Canada, reported in 1921 that *A. pauciflorum* (*A. tenerum* Vasey) was self-fertile, and White (Y. B. Q.) found this species almost completely self-fertile and showing no loss in vegetative vigor from continued selfing. This condition presents a strange contrast to the behavior of *A. cristatum*. Beddows (*3*), of Wales, agrees with White, finding both *A. repens* and *A. pauciflorum* highly self-fertile.

Bentgrass (*Agrostis* spp.): North (Y. B. Q.), formerly of Rhode Island, reported *A. alba* (redtop) somewhat more self-fertile than *A. tenuis* (colonial bent), *A. canina* (velvet bent), or *A. palustris*

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Huds. (creeping bent). All of the *Agrostis* species showed a tendency toward loss of vigor from continued selfing although only a few generations were obtained.

Smooth bromegrass (*Bromus inermis*): White (Y. B. Q.) reports self-sterility "fairly marked" in bromegrass, but adds that there is a wide variation between plants. If this variation exists it would admit of the development of reasonably self-fertile strains. Beddows' (*3*) results show a very high degree of self-sterility in *B. inermis*, but very little in *B. catharticus* (*B. unioloides*) and other annual bromes. White also reports a marked and progressive loss in vegetative vigor from selfing for four or five generations. This loss of vigor from selfing is confirmed by McConkey (Y. B. Q.), of the Ontario Agricultural College.

Reed or tall fescue (*Festuca elatior* var. *arundinacea*): Beddows (*3*) found 5.1 times as many seeds developing in open-pollinated as in close-pollinated inflorescences. Govaert (Y. B. Q.), of the Rijksstation voor Plantenveredeling, Ghent, Belgium, reports a wide variation between individual plants, some being almost completely self-fertile.

Meadow fescue (*Festuca elatior* var. *pratensis*): According to Beddows (*3*), the meadow fescue is more self-sterile than the tall fescue. Open-pollinated panicles gave 22.3 times as many seed as the close-fertilized ones. As in the tall fescue, however, Govaert (Y. B. Q.), of Belgium, found a wide variation in individual plants, the number of seeds on different plants varying from an average of less than 1 to 409 per inflorescence. There would seem, therefore, to be an opportunity here to select self-fertile strains. G. Nilsson-Leissner (Y. B. Q.), at the Swedish Seed Association, Svalöf, Sweden, found cases of complete self-sterility in meadow fescue and a marked loss of vigor after repeated selfing.

Red fescue (*Festuca rubra*): Beddows (Y. B. Q.) found the self-fertility in red fescue about as low as in tall fescue, selfed plants producing about one-fifth as much seed as those open-pollinated. G. Nilsson-Leissner (Y. B. Q.), of Svalöf, found cases of complete self-sterility and a marked loss of vigor caused by selfing, as he had in meadow fescue.

Canada bluegrass (*Poa compressa*): McConkey (Y. B. Q.), of the Ontario Agricultural College, reports this species largely self-fertile. Under such conditions there is probably very little decrease in vegetative vigor caused by selfing.

Kentucky bluegrass (*Poa pratensis*): A considerable number of plant breeders and cytologists have studied this important grass and found it unusually interesting from two angles—there is a wide variation in the number of chromosomes, and seed is produced, to a considerable extent at least, apomictically. Musser (Y. B. Q.), of Pennsylvania, Brown (Y. B. Q.), of Missouri, and others report no self-sterility in Kentucky bluegrass and no apparent loss of vigor from selfing.

Sudan grass (*Sorghum vulgare* var. *sudanense*): Sudan grass, a close relative of the cultivated sorghums, is self-fertile. Robertson (Y. B. Q.), of Colorado, reports no apparent loss of vigor after three generations of selfing. Wenholz (*36, p. 33*), of New South Wales, reports loss of vigor in some lines under continued inbreeding.

Fruwirth (*5*) reports a method of overcoming the handicap of self-sterility in the perennial grasses that may be of great value to plant breeders. He divided the clump or tuft that had developed from a single seed and grew these parts of the same plant to maturity in separate pots or boxes. When these individual plants were isolated as a group and allowed to bloom freely and interpollinate each other, considerable viable seed was produced. There were, however, some cases where this method was not successful. With "French ryegrass" no seed was obtained, and Fruwirth concluded that these plants were completely self-sterile.

Self-Sterility in Hybrids

Self-sterility, or more properly male-sterility, in the F_1 of interspecific and intergeneric grass hybrids is quite common (table 4). In many cases there is variation in the degree of sterility among individuals, but in most cases backcrossing is required to produce seed. The number of self-fertile segregates increases with repeated backcrossing, which is an accepted procedure among breeders who are laboring to produce new varieties of value in practical agriculture. In some cases polyploidy is induced and increased vigor obtained by crossing the hybrid with a third species.

Verushkine (*35*) reports that in general the fertility of the hybrids of *Triticum* and *Agropyron* exceed considerably the fertility of the rye-wheat hybrids, and that it is somewhat higher than the fertility of *Aegilops* × *Triticum* hybrids. He classifies the *Triticum* × *Agropyron* hybrids into the following groups in respect to the fertility of the first generation:

1. *T. vulgare* [12] × *A. elongatum.*
2. *T. durum* × *A. intermedium* and *A. trichophorum.*
3. *T. vulgare* [12] × *A. intermedium* and *A. trichophorum.*
4. *T. durum* × *A. elongatum.*

No trouble is experienced in the first group in obtaining self-fertilized seed, but in the fourth group "among hundreds of plants" Verushkine and his associates found none self-fertile.

Successful crosses of the two genera *Festuca* and *Lolium* are reported by T. J. Jenkin (see footnotes 1 and 3, table 4), of the Welsh Plant Breeding Station. In many cases although seed set, none of it germinated. In other cases F_1 plants were established, but these were male-sterile. They were, however, in many cases used successfully as the pistillate parent in backcrosses on one of the parent species.

Chromosome Complex of Grasses

The basic chromosome number for grasses is usually seven. There are, of course, exceptions, like that of the *Sorghum* species, where the basic number is five. Cytologists have already determined the chromosome number in a large proportion of the grass species, and their summarized records are available to the plant breeder in several publications. The most extensive lists of chromosome numbers in grasses are those of Avdulow (*2*), Gaiser (*6*), and Tischler (*30*). In order to make such data available to breeders in the United States, a condensed list of reported chromosome numbers in grasses is given in table 5.

[12] Synonym for *T aestivum.*

No thorough investigation of the chromosome behavior during meiosis has been made for any of the forage grasses. A limited amount of information is available, however, regarding valence, lagging, etc., of the chromosomes of certain grasses. Wide differences in the chromosome numbers of individuals of certain species have been reported. These chromosome irregularities naturally affect the behavior of hybrids and in some cases are useful factors in maintaining the purity of selected strains. Thus in breeding orchard grass (*Dactylis glomerata*) the Ontario Agricultural College (*23*) found the leafy pasture strain had 14 chromosomes while the common commercial strain had 28 chromosomes. Therefore the two strains do not cross readily; each remains pure or distinct.

The pasture strain of orchard grass developed by selection in Ontario has 14 chromosomes, the same number as the so-called wild species *Dactylis aschersoniana*, according to Müntzing (*20*) of the Swedish Seed Association. Müntzing found natural crosses of *D. glomerata* and *D. aschersoniana* near Svalof, although it was found very difficult to make this cross artificially. He found 21 chromosomes in the natural hybrid, and when this triploid was backcrossed on *D. glomerata* the F_1 had 35 chromosomes. These pentaploids were more vigorous than ordinary orchard grass, and in their progeny individuals were found having 38, 39, and even 41 chromosomes. Peto (*24*), at the University of Alberta, in his very detailed cytological studies of the *Agropyron* species, reported 14 and 28 chromosome forms of *A. cristatum* and 21 and 28 chromosome forms of *A. pauciflorum*.

Randolph (Y. B. Q.), cytologist, Division of Cereal Crops and Diseases, Bureau of Plant Industry, at Cornell University, found in Kentucky bluegrass (*Poa pratensis*) individuals having 48, 50, 54, 68, and 72 somatic chromosomes. The most common number reported for *P. pratensis* is 56. Practically all cytologists who have worked with this species have noted wide variations. Since 7 is the basic chromosome number in most grasses, if this condition is a tendency toward polyploidy the differences should be various multiples of 7. Randolph's results previously mentioned and those of Rancken (*26*) may be explained on the basis that these indicated variations from exact multiples of 7 are the result of the cytologists' failure to distinguish between whole chromosomes and fragments. These "supernumerary chromosome fragments" Rancken reports are present in *Poa pratensis*, *Dactylis glomerata*, *Festuca elatior* var. *pratensis*, and *Alopecurus pratensis*. Chromosome fragments, Rancken believes, may possibly act as phylogenetic factors.

A peculiar chromosome relationship found in *Phalaris* species is reported by Jenkin and Sethi (*15*). *P. arundinacea* and *P. tuberosa* both have 28 somatic chromosomes showing 14 bivalents in the heterotypic metaphase. The basic number in these species is obviously 7, but in *P. canariensis* the basic number is reported as 6. *P. arundinacea* and *P. tuberosa* were successfully crossed and the F_1 had 28 chromosomes, 12 bivalent and 4 univalent. Other instances of apparent aberrant chromosome conditions are recorded by cytologists, but those mentioned are sufficient to indicate the nature of such abnormalities in forage grasses.

The production of polyploidy or doubling of the chromosome number by means of species crosses is illustrated by the work of Nilsson (*21*), Undrom, Sweden, who reports as follows: "From the hybrid *F.* [*Festuca*] *arundinacea* × *F. gigantea*, which is highly sterile, 2 progeny plants were obtained. F_1 had the same somatic chromosome number (42) as the parents, but the progeny plants differed very much, one having the somatic number 84." This doubling of the chromosomes is explained to have originated by accidental intercrossing of the F_1 hybrid and a third species, *F. elatior* var. *pratensis*. Such an explanation is said to be in harmony with the morphological characters. The author claims this has resulted in "a new polyploid type intermediate between the parents and highly fertile in comparison with F_1."

Compatibility a Factor in Hybridization

As hydridization investigations progress it is apparent that there are different degrees of compatibility not only between species but also between varieties and even strains. Thus Armstrong (*1*), when using *Agropyron glaucum* as the pollen parent, was 32.2 to 34.6 percent successful with *Triticum durum* and *T. dicoccum*, respectively, as the pistillate parents and only 6.5 to 11.7 percent successful with three varieties of *T. aestivum* as the pistillate parent. Strain no. 820 of *A. elongatum* crosses on emmer (*T. dicoccum*) resulted in 38.7 percent success, while strain no. 1083 crossed with emmer gave only 1.5 percent success.

Most workers have found a high degree of compatibility between *Triticum aestivum* and *Agropyron elongatum* and between *T. durum* or *T. dicoccum* and *A. intermedium*. *A. trichophorum* and *A. junceum* are also said to cross readily with wheat, but no one has been able to cross wheat with *A. repens*, and Sando[13] reports failure in his attempts to cross wheat and *A. smithii*. Armstrong (*1*) and other Canadian workers have failed in their attempts to use as the pollen parent *A. desertorum*, *A. dasystachyum*, *A. caninum*, *A. imbricatum*, *A. repens*, *A. cristatum*, or *A. richardsoni* in crosses on *T. durum*, *T. dicoccum*, or *T. aestivum*. These unsuccessful attempts to combine the indicated species of *Agropyron* with the *Triticum* species, while not conclusive, are evidence of incompatibility not apparent from morphological characters customarily used in botanical classifications. The examples given of differences between species of *Agropyron* and *Triticum* will serve to illustrate what the breeder may expect to encounter in other genera.

Technique of Hybridization

Jenkin, of the Welsh Plant Breeding Station, has, no doubt, studied this question to a greater extent than any other investigator. His recommendations (*9*) as to the best methods of crossing grasses are given in a bulletin published in 1924, and a later résumé (*11*) of the subject was published in 1931.

Geneticists usually agree that hand-crossing is the only method to follow if dependable results are to be obtained, and this is emphasized by Jenkin. He sets forth several rules to be observed in the work of hybridization:

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[13] Personal correspondence, 1936.

1. No inflorescence of a species used for crossing should be allowed to flower unprotected in the greenhouse. This is to avoid free pollen floating about.

2. All ventilators should be closed an hour or more before starting operations, to prevent drafts and allow free pollen to settle and avoid scattering pollen that is being collected for use in crossing.

3. Soft brushes should be used in applying pollen.

4. On both the pistillate and the pollen parent inflorescences should not be exposed any longer than absolutely necessary.

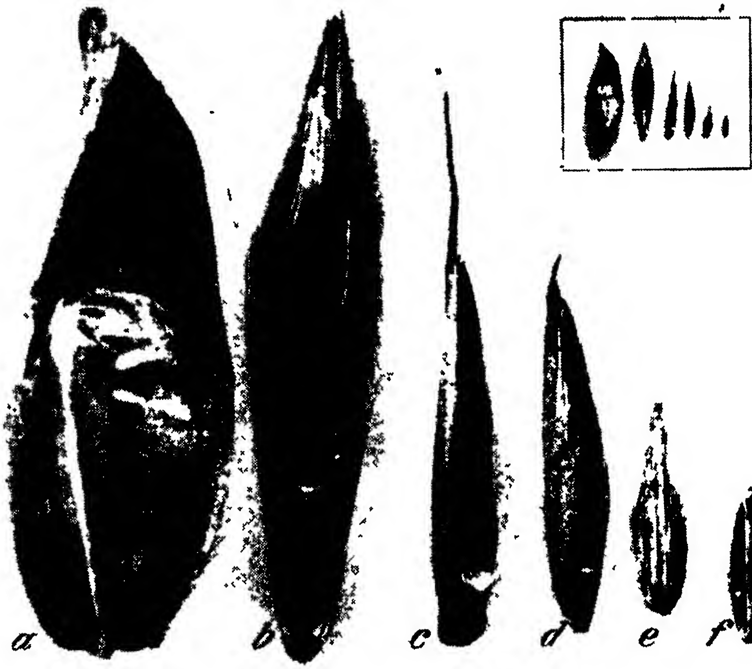

Figure 24.—Comparative size of florets of various grasses in comparison with the wheat floret: *a*, Wheat; *b*, smooth bromegrass; *c*, crested wheatgrass; *d*, orchard grass; *e*, woolly fingergrass; *f*, Kentucky bluegrass. × 9. Upper right natural size.

5. Each brush should be sterilized after being used, and a sufficient number of brushes should be available so that no brush will be used more than once a day.

Emasculation Methods and Equipment

Emasculation of all flowers left on the pistillate parent to be pollinated is necessary except when that parent is known to be completely male-sterile. This operation must perforce be performed before full bloom occurs, but it is most easily accomplished just prior to this stage of development. In sorghums the flowers may be successfully emasculated by immersing the inflorescence in hot water for a short time. This method, discovered by Stephens and Quinby (*28*), may perhaps be equally effective on the smaller grasses, but until the exact temperatures required to kill the pollen on these grasses without

injuring the stigmas are determined, most breeders will continue to use the more tedious hand-emasculation method.

The process of hand emasculation in grasses is very difficult owing to the small size of the individual florets (fig. 24). While Jenkin suggests emasculating with the naked eye or with the assistance of only a small hand lens, most breeders find magnifying instruments necessary or at least very helpful. Instruments for this purpose should be capable of use without being held in the hand, since both hands must be free to manipulate the flowers. Magnifying glasses provided with a contrivance to hold them in position on the operator's head are preferred by some. Others find binocular microscopes attached to a horizontal arm on a vertical stand of the proper height most satisfactory for this work (fig. 25). When the lenses are adjusted to a long focus there is little interference with the movements of the hands and the delicate emasculation operations may be carried out with more assurance than without such equipment. The use of a binocular in hybridization work with grasses was suggested in 1934 by De Villiers (*4*), research officer, Division of Plant Industry, Pretoria, South Africa. Much of his work was with the *Digitaria* species, or woolly fingergrasses, which have extremely small flower parts (fig. 24). Emasculation of such grass flowers without magnifying instruments is well-nigh impossible.

Figure 25.—A binocular microscope with horizontal arm adjustment as used in the emasculation of woolly fingergrass for cross-pollination in the greenhouse.

The technique that Sando (Y. B. Q.) developed in the hybridization of *Triticum* and *Agropyron* species is applicable to other grasses. The necessary operations are described as follows: In preparing a plant for hybridization, several upper and lower spikelets of the inflorescence are excised with a small scissors before blooming. Likewise all but the two lower florets of the remaining spikelets are removed. Emasculation of these flowers is then effected with slender tweezers and the inflorescence enclosed in a glassine bag. Several days later,

when the stigmas reach the stage of receptivity, the glassine bag is removed and pollinations are made, after which the bag is again replaced to remain until maturity.

In the transfer of pollen the most successful results have been accomplished by holding a sheet of clean paper beneath the blooming flowers and slightly shaking them to cause the anthers to expel their pollen. This pollen is then placed in a convenient ring receptacle

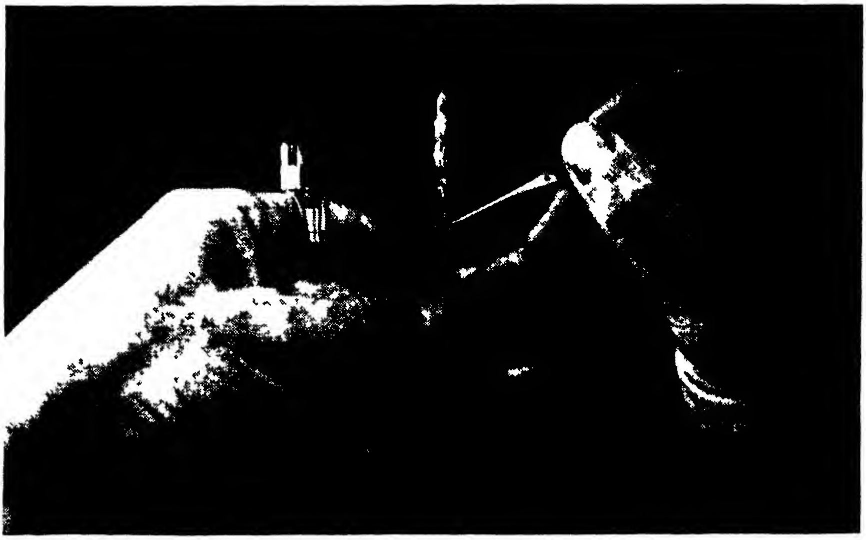

Figure 26.—A handy pollen carrier devised by W. J. Sando, United States Department of Agriculture, consisting of an adjustable ring in which are inserted capsules that may be readily removed and discarded after the pollination process is completed.

(fig. 26), described in a previous publication (*17*). From this receptacle it is transferred with a pair of tweezers or otherwise to the stigmas of the flowers previously emasculated. The period of pollen production Sando finds can be extended considerably by the following practice: Holding a culm just below the inflorescence with the left hand, the head is stroked upward vigorously several times with the thumb and forefinger of the right hand. This induces the flowers to extrude their anthers, provided the temperature is favorable. Such artificial stimulation is most readily accomplished previous to the active blooming periods rather than later. High humidity or rainfall causes the pollen to form a conglomerate mass through the absorption of moisture from the atmosphere. Such pollen is nonfunctional and therefore useless in hybridization.

Collecting the Pollen and Pollinating

It will be noted in the previous discussion that Sando applies the pollen with tweezers while Jenkin prefers to use a soft brush. In collecting the pollen also Jenkin merely shakes the bagged heads until all the pollen grains are detached from the anthers and then pours the pollen out of the bag on a sheet of paper previously creased so

that it can be folded easily to collect the pollen in the middle of the sheet.

The time of day when anthesis takes place in various grasses has been discussed under flowering habits. When two species or two genera are being crossed, difficulty is sometimes encountered because the pollen parent does not reach the blooming stage at the same date as the pistillate parent. Some adjustment of the blooming period in most grasses may be effected by subjecting one or both parents to an artificial regulation of the day length. Sando (Y. B. Q) used this method successfully to bring his *Agropyron elongatum* plants into bloom at the time his wheat plants were ready to cross-pollinate.

The length of time pollen grains will remain viable depends altogether on the conditions in which they are kept. When properly stored they have been known to remain viable several days, but the safest procedure is to apply the pollen immediately after it is gathered. More latitude exists in respect to the receptivity of the stigmas. Stephens and Quinby (*29*) report for sorghums that "stigmas were receptive at least 48 hours before the flowers bloomed and from 8 to 16 days after blooming." Jenkin (*9*) reports for *Lolium perenne* that the stigmas were receptive in one case 13 days after emergence, but none were found receptive on the fifteenth day. It is apparent therefore that considerable time may elapse before pollen need be applied to the stigmas.

While Jenkin advises repeated application of pollen, his data show as good results from two applications as from four or six. It would seem, therefore, that if the pollen is in good condition and is properly and thoroughly applied, one replication is sufficient.

Isolation Methods and Materials

When hybridization is being conducted in a greenhouse, ordinary glassine or waxed paper bags have proved satisfactory for isolating the inflorescences of parent plants. For field operations, however, Jenkin (*11*) found the glassine bags, as used in the greenhouse, useless, and ordinary parchment paper bags equally unreliable. Cloth bags woven in seamless pillowcase form and held in place by specially constructed frames proved most satisfactory. Extensive tests were made of various cotton fabrics, and it was found that many of these did not fully prevent the passage of pollen grains. However, Jenkin found a satisfactory standard fabric, the specifications of which are: Threads per inch—warp 68, weft 65; count—warp 2/32's, weft 16's.

Cages are also used in the field to prevent unintended pollination, and special ventilated rigid boxes which may be adjusted over a single culm have been constructed and used by some breeders. The latter, however, are too expensive for extensive use. All experienced breeders agree that unless great care is used in bagging, the results of otherwise careful work may be vitiated by unfavorable conditions within the bag. Failure of bagged heads to produce seed is in many cases caused by these unfavorable conditions rather than by incompatibility of the parents.

Inheritance of Characters

Only a very limited amount of data is available on this subject. Those who have studied *Triticum-Agropyron* hybrids agree that the perennial nature of the *Agropyron* parent is dominant in the F_1 hybrid. The proportion of perennials quite naturally decreases rapidly in succeeding generations of backcrosses on the annual *Triticum* species. According to Verushkine (*35*), only 43 to 66 percent of the second generation plants are perennials. He remarks that the F_2 affords a wide segregation of characters and includes for the most part intermediate types.

Armstrong (*1*), of the Central Experimental Farm, Ottawa, Canada, agrees with Verushkine in general as to the dominance of the perennial character in the *Triticum-Agropyron* hybrids. He names several other *Agropyron* characters that are dominant, but finds a condition of intermediacy in respect to quantitative characters such as spike density, glume width, and leaf width and scabrousness. When awned wheats were used as the pistillate parent and *A. glaucum* as the pollen parent, the hybrids were awn-tipped, an intermediate condition. When *A. elongatum* was used as the pollen parent the hybrids were awnless in most cases. Both species of *Agropyron* are awnless.

The presence in *Lolium multiflorum* of a root substance that causes a fluorescence on filter paper when examined under ultraviolet light has been used to distinguish this species from *L. perenne*. Woodforde (*39*), of the Tasmanian Department of Agriculture, reports that this character is inherited as a simple Mendelian dominant dependent on a single factor. However, he found no genetic linkage between fluorescence and awned flowering glumes, a distinguishing character of *L. multiflorum*.

Jenkin (*12*), of the Welsh Plant Breeding Station, in a study of bulbous tall oatgrass, found in the F_1 of a cross of the nonbulbous and bulbous forms an intermediate condition in respect to bulb development, although all F_1 plants were definitely bulbous. In the F_2 and F_3 there was an apparent segregation for bulb development, which was hard to analyze, since a great majority of the plants were more or less bulbous. He concludes that more than one pair of factors is concerned in bulb development, and that the same is true of the hairiness of stem nodes, another distinguishing character of bulbous tall oatgrass. The value of this research lies in the fact that the bulbous form behaves as a weed in cereal fields under certain conditions, while the nonbulbous form does not.

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APPENDIX

TABLE 1.—*Development centers of important grasses useful in breeding* [1]

Region	Grasses [2]: Common name	Grasses [2]: Scientific name
(1) Europe, except the Mediterranean region and the eastern or dry portion of the Union of Socialist Soviet Republics.	Redtop	*Agrostis alba.*
	Bentgrass	*Agrostis* spp.
	Beachgrass	*Ammophila areanaria.*
	Tall oatgrass	*Arrhenatherum elatius.*
	Awnless bromegrass	*Bromus inermis.*
		Dactylis aschersoniana.
	Cocksfoot or orchard grass	*D. glomerata.*
	Reed or tall fescue	*Festuca elatior* var. *arundinacea.*
	Meadow fescue	*F. elatior* var. *pratensis.*
	Italian ryegrass	*Lolium multiflorum.*
	Perennial ryegrass	*L. perenne.*
	Mountain timothy	*Phleum alpinum.*
		P. boehmeri.
	Timothy	*P. pratense.*
	Mountain bluegrass	*Poa alpina.*
	Annual bluegrass	*P. annua.*
	Canada bluegrass	*P. compressa.*
	Kentucky bluegrass	*P. pratensis.*
	Rough-stalked bluegrass	*P. trivialis.*
	Cordgrass	*Spartina townsendii.*
(2) Mediterranean region of Europe and Africa.	Giant reed	*Arundo donax.*
	Wild oats (annuals)	*Avena barbata, A. fatua, A. sterilis, A. strigosa.*
	Bromes (annuals; cheat or chess)	*Bromus arvensis, B. mollis, B. secalinus, B. sterilis.*
	Red fescue	*Festuca rubra.*
	Canary grass	*Phalaris canariensis.*
	Harding grass	*P. tuberosa.*
	Esparto grass	*Stipa tenacissima.*
(3) Eastern Union of Socialist Soviet Republics and Siberia.	Wheatgrasses	*Agropyron caninum, A. cristatum, A. ehongatum, A. intermedium, A. trichophorum.*
	Reedgrasses	*Calamagrostis* spp.
	Wild-rye	*Elymus* spp.
	Sheep fescue	*Festuca ovina.*
	Ricegrasses	*Oryzopsis* spp.
	Chee grass	*Stipa splendens.*
(4) Southern Union of Soviet Socialist Republics, Turkistan, Sinkiang (China), Turkey, Palestine, and Afghanistan.	Goatgrasses	*Aegilops crassa, A. cylindrica, A. ovata, A. squarrosa, A. triuncialis.*
	Meadow foxtail	*Alopecurus pratensis.*
	Sweet vernal grass	*Anthoxanthum odoratum.*
	Wild oats	*Avena barbata, A. fatua, A. sterilis, A. strigosa.*
	Red fescue	*Festuca rubra.*
	Barley relatives	*Hordeum species.*
	Bulbous bluegrass	*Poa bulbosa.*
	Rye	*Secale cereale.*
	Johnson grass	*Sorghum halepense.*
	Wheat relatives	*Triticum* spp.
(5) Tibet, western provinces of China, and eastern Mongolia.	Wheatgrasses	*Agropyron* spp.
	Wild-ryes	*Elymus* spp.
	Fescues	*Festuca* spp.
	Bluegrasses	*Poa alpina, P. attenuata, P. nemoralis, P. tibetica.*
	Needlegrasses	*Stipa* spp
(6) Eastern Siberia, Manchuria, northeastern China, Chosen, and Japan.		*Arundinella* spp.
	Manchu reedgrass	*Calamagrostis epigeios.*
	Jungle rice	*Echinochloa colona.*
	Japanese millet	*E. crus-galli.*
	Broomcorn millet	*Panicum miliaceum.*
	Foxtail millet	*Setaria italica.*
	Bristlegrasses	*Setaria* spp.
	Japanese lawngrass	*Zoysia japonica.*
	Manila lawngrass	*Z. matrella.*
	Sorghums	*Sorghum vulgare.*

[1] Numbers of regions correspond to those in fig. 1.

[2] In naming the grasses characteristic of a region no attempt has been made to restrict them to native species, since in certain areas the introduced species are more abundant and more important than the native ones. Some grasses, omitted because of their apparent lack of usefulness, are more widely distributed and more characteristic of a region than are any of the species named. It should be understood also that in most cases other species of the genera listed occur in the region.

TABLE 1.—*Development centers of important grasses useful in breeding*—Continued

Region	Grasses	
	Common name	Scientific name
(7) India, southeastern China, Burma, Malay Peninsula, Sumatra, Java, Borneo, New Guinea, Taiwan.	Angleton grass	*Andropogon annulatus.*
	Dwarf bamboo	*Bambusa nana.*
	Bamboo	*B. vulgaris.*
	"Doob" (Bermuda) grass	*Cynodon dactylon.*
	Finger millets	*Eleusine coracana.*
	Centipede grass	*Eremochloa ophiuroides.*
	Cogon grass	*Imperata cylindrica.*
	Ricegrass	*Oryza sativa.*
	Kutki millet	*Panicum psilopodium.*
	Koda millet	*Paspalum scrobiculatum.*
	Edible bamboo	*Phyllostachys edulis.*
	Sugarcane relatives	*Saccharum* spp.
	Sorghums	*Sorghum vulgare.*
(8) Australia, New Zealand, and Tasmania.	Native grasses (grown in dry areas):	
	Mitchell grass	*Astrebla pectinata.*
	Curly Mitchell grass	*A. triticoides*
	Wallaby grass	*Danthonia semiannularis.*
	Flinders grass	*Iseilema membranacea.*
	Australian tussock grass	*Poa caespitosa.*
	New Zealand tussock grass	*P. flabellata.*
	Silvery sandgrass	*Spinifex hirsuta.*
	Kangaroo grass	*Themeda* spp.
	Spinifex	*Triodia* spp.
	Introduced grasses (grown where rainfall is adequate).	
	Rhodes grass	*Chloris gayana.*
	Orchard grass	*Dactylis glomerata.*
	Meadow fescue	*Festuca pratensis.*
	Italian ryegrass	*Lolium multiflorum.*
	Perennial ryegrass	*L. perenne.*
	Dallis grass	*Paspalum dilatatum.*
(9) Equatorial Africa	Bluestem relatives	*Andropogon* spp.
	Brachiarias	*Brachiaria* spp.
	Teff	*Eragrostis abyssinica.*
	Carib grass	*Eriochloa polystachya.*
	Wild barleys	*Hordeum* spp.
		Hyparrhenia spp.
	Guinea grass	*Panicum maximum.*
	Para grass	*P. purpurascens.*
	Bentham grass	*Pennisetum benthami.*
	Kikuyu grass	*P. clandestinum.*
	Pearl or cattail millet	*P. glaucum.*
	Merker grass	*P. merkeri.*
	Napier or elephant grass	*P. purpureum.*
	Sorghums	*Sorghum vulgare.*
	Grass sorghums	*S. vulgare* vars.
	"Rooi gras" or red grass	*Themeda triandra.*
	Herringbone grass	*Urochloa pullulans.*
(10) Africa south of 10° south latitude, which includes southern Angola and Tanganyika, all of Nyassaland, Mozambique, Rhodesia, Bechuanaland, South Africa, and Madagascar.	Rhodes grass	*Chloris gayana.*
	"Kweek" (Bermuda) grass	*Cynodon dactylon.*
	Red kweek grass	*C. hirsutus.*
	Woolly fingergrass	*Digitaria eriantha stolonifera.*
	Other fingergrasses	*Digitaria* spp.
		Ehrharta calycina.
		Hyparrhenia spp.
	Sorghums	*Sorghum vulgare.*
	Grass sorghums	*S. vulgare* vars.
	"Rooi gras" or red grass	*Themeda triandra.*
	Natal grass	*Tricholena rosea.*
(11) Brazil, eastern Bolivia, Paraguay, Uruguay, and northeastern Argentina.	Carpet grass	*Axonopus compressus.*
	Pampas grass	*Cortaderia selloana.*
	Jaragua grass	*Hyparrhenia rufa.*
	Molasses grass	*Melinis minutiflora.*
	Rice	*Oryza sativa.*
	Guinea grass	*Panicum maximum.*
	Bahia grass	*Paspalum notatum.*
(12) Andean region of Peru, Bolivia, Chile, and Argentina.	"Maicillo" or "cachi"	*Axonopus scoparius.*
	Reedgrasses	*Calamagrostis* spp.
	Fescues	*Festuca* spp.
	Muhly grass	*Muhlenbergia* spp.
	Bluegrasses	*Poa* spp.
(13) Southern Mexico, Central America, northwestern South America, and the West Indies.	Giant reed	*Arundo donax.*
	Carpet grass	*Axonopus compressus.*
	"Malojilla" or Carib grass	*Eriochloa polystachya.*
	Teosinte	*Euchlaena mexicana.*

TABLE 1.—*Development centers of important grasses useful in breeding*—Continued

Region	Grasses: Common name	Grasses: Scientific name
	Mexican teosinte	*E. perennis.*
	Wild rice	*Oryza latifolia.*
	Guinea grass	*Panicum maximum.*
	Para grass	*P. purpurascens.*
	Bahia grass	*Paspalum notatum.*
	St. Augustine grass	*Stenotaphrum secundatum.*
	Eastern gamagrass	*Tripsacum dactyloides.*
	Long-leaved gamagrass	*T. latifolium.*
	Guatemala grass	*T. laxum.*
	Corn (maize)	*Zea mays.*
(14) Great Plains and intermountain regions of North America.	Native grasses:	
	Thickspike wheatgrass	*Agropyron dasystachyum.*
	Slender wheatgrass	*A. pauciflorum.*
	Streambank wheatgrass	*A. riparium.*
	Bluestem (western wheatgrass).	*A. smithii.*
	Bluebunch wheatgrass	*A. spicatum.*
	Bearded wheatgrass	*A. subsecundum.*
	Big bluestem	*Andropogon furcatus.*
	Turkeyfoot	*A. hallii.*
	Silver beardgrass	*A. saccharoides.*
	Little bluestem	*A. scoparius.*
	Six-weeks grama	*Bouteloua barbata.*
	Crowfoot grama	*B. chrondrosioides.*
	Side-oats grama	*B. curtipendula.*
	Black grama	*B. eriopoda.*
	Hairy grama	*B. hirsuta.*
	Rothrock grama	*B. rothrockii.*
	California bromegrass	*Bromus carinatus.*
	Buffalo grass	*Buchloë dactyloides.*
	Pine grass	*Calamagrostis rubescens.*
	Long-leaved sandgrass	*Calamovilfa longifolia.*
	Canada wild-rye	*Elymus canadensis.*
	Giant wild-rye	*E. condensatus.*
	Beardless wild-rye	*E. triticoides.*
	Virginia wild-rye	*E. virginicus.*
	Bluebunch fescue	*Festuca idahoensis.*
	Six-weeks fescue	*F. octoflora.*
	Sheep fescue	*F. ovina.*
	Red fescue	*F. rubra.*
	Greenleaf fescue	*F. viridula.*
	Curly mesquite	*Hilaria belangeri.*
	Galleta grass	*H. jamesii.*
	Junegrass	*Koeleria cristata.*
	Switchgrass	*Panicum virgatum.*
	Canby bluegrass	*Poa canbyii (P. laevigata).*
	Nevada bluegrass	*P. nevadensis.*
	Sandberg bluegrass	*P. secunda (P. sandbergii).*
	Nuttall alkali-grass	*Puccinellia nuttalliana.*
	Blowout grass	*Redfieldia flexuosa.*
	Indian grass	*Sorghastrum nutans.*
	Alkali sacaton	*Sporobolus airoides.*
	Sand dropseed	*S. cryptandrus.*
	Sacaton	*S. wrightii.*
	Long-awned spear grass	*Stipa comata.*
	Introduced grasses:	
	Crested wheatgrass	*Agropyron cristatum.*
	Awnless bromegrass	*Bromus inermis.*
	Bulbous bluegrass	*Poa bulbosa.*
	Sudan grass	*Sorghum vulgare* var. *sudanense.*
(15) Southeastern Canada and northeastern United States.	Native grasses:	
	Quackgrass	*Agropyron repens.*
	American beachgrass	*Ammophila breviligulata.*
	Big bluestem	*Andropogon furcatus.*
	Little bluestem	*A. scoparius.*
	Bluejoint	*Calamagrostis canadensis.*
	Virginia wild-rye	*Elymus virginicus.*
	American mannagrass	*Glyceria grandis.*
	Switchgrass	*Panicum virgatum.*
	Reed canary grass	*Phalaris arundinacea.*
	Smooth cordgrass	*Spartina alterniflora.*
	Big cordgrass	*S. cynosuroides.*
	Saltmeadow cordgrass	*S. patens.*
	Prairie cordgrass	*S. pectinata.*
	Eastern gamagrass	*Tripsacum dactyloides.*
	Wild rice	*Zizania aquatica.*

TABLE 1.—*Development centers of important grasses useful in breeding*—Continued

Region	Grasses: Common name	Grasses: Scientific name
(16) Southeastern United States.	Introduced grasses (see also list for region 1):	
	Japanese millet	*Echinochloa crus-galli* var. *frumentacea*.
	Foxtail millet	*Setaria italica*.
	Native grasses:	
	Southern cane	*Arundinaria gigantea*.
	Small cane	*A. tecta*.
	Virginia wild-rye	*Elymus virginicus*.
	Texas bluegrass	*Poa arachnifera*.
	Smooth cordgrass	*Spartina alterniflora*.
	Big cordgrass	*S. cynosuroides*.
	Saltmeadow cordgrass	*S. patens*.
	Southern cordgrass	*S. spartinae*.
	Eastern gamagrass	*Tripsacum dactyloides*.
	Southern wild rice	*Zizaniopsis miliacea*.
	Introduced grasses:	
	Carpet grass	*Axonopus compressus*.
	Rescue grass	*Bromus catharticus*.
	Bermuda grass	*Cynodon dactylon*.
	Centipede grass	*Eremochloa ophiuroides*.
	Para grass	*Panicum purpurascens*.
	Dallis grass	*Paspalum dilatatum*.
	Bahia grass	*P. notatum*.
	Vasey grass	*P. urvillei*.
	Pearl millet	*Pennisetum glaucum*.
	Napier grass	*P. purpureum*.
	Japanese cane	*Saccharum chinense*.
	Johnson grass	*Sorghum halepense*
	Natal grass	*Tricholaena rosea*.

TABLE 2.—*Objectives and progress in the selective breeding of grasses as reported by workers in the United States and Canada*

Location [1]	Individual workers	Genera and species	Period work under way	Objectives	Success attained
UNITED STATES					
Arizona:					
Tucson*	E. W. Hardies	*Bouteloua curtipendula, B. eriopoda, B. gracilis, Hilaria belangeri, H. jamesii, H. mutica, H. rigida, Muhlenbergia porteri, Oryzopsis coerulescens, O. hymenoides, O. miliacea, Setaria macrostachya.*	1936 (continued)	Increased seed and forage production, longevity, and drought resistance.	
California:					
Davis	L. G. Goar	*Sorghum vulgare* var. *sudanense.*	5 years	Increased hay and pasture production	Much.
Colorado:					
Colorado Springs*	E. W. Hardies	*Agropyron smithii*	1936 (continued)	Increased seed and forage production, longevity, and drought resistance.	Many promising variants found.
Fort Collins	Alvin Kezer	*Bromus inermis*	1910–14	Increased yield of forage	
	D. W. Robertson and Otto Coleman.	*Sorghum vulgare* var. *sudanense.*	1934 (continued)	(a) Yield and uniformity of seed; (b) reduced hydrochloric acid content.	(a) Much.
Florida:					
Gainesville*	G. E. Ritchey and W. E. Stokes.	*Axonopus compressus*	10 years	(a) Increased pasturage value; (b) reduced stolon development.	(a) Much; (b) little.
		Axonopus furcatus	do	Increased pasturage value	Much.
		Cynodon spp.		do	Medium to much.
		Digitaria spp.	1933 (continued)	Increased seed production and pasturage value.	Medium.
		Eremochloa ophiuroides	1931 (continued)	Increased seed production, pasturage, and lawn value.	Much.
		Melinis minutiflora	1933 (continued)	(a) Increased pasturage value, (b) early seed production; (c) winter hardiness.	(a) Much, (b) and (c) little.
	G. E. Ritchey and F. H. Hull.	*Paspalum notatum*	do	Increased pasturage value and disease resistance.	Much.
	G. E. Ritchey and W. E. Stokes.	*Pennisetum purpureum*	1934 (continued)	Increased pasturage and silage value and resistance to leaf spot.	Do.
Georgia:					
Tifton* (Coastal Plain Experiment Station).	J. L. Stephens and G. W. Burton.	*Cynodon dactylon*	1929 (continued)	Increased hay and pasture production and winter hardiness.	Medium.
		Cynodon spp.	1936 (continued)	Increased seed production, palatability, and winter hardiness.	
		Digitaria spp.		Increased viable seed production, better turf, and winter hardiness.	
		Panicum antidotale		Production of nonshattering seed heads	

[1] Except where otherwise noted, the work is conducted at the State Agricultural Experiment Station. An asterisk (*) indicates cooperation between the U. S. Department of Agriculture and the State agricultural experiment station.

Table 2.—*Objectives and progress in the selective breeding of grasses as reported by workers in the United States and Canada*—Continued

Location	Individual workers	Genera and species	Period work under way	Objectives	Success attained
UNITED STATES—continued					
Georgia—Continued Tifton [a] (Coastal Plain Experiment Station)	J. L. Stephens and G. W. Burton	*Panicum purpurascens*		Winter hardiness and earliness	
		Paspalum dilatatum		Increased production of viable seed, leafiness, and disease resistance	
		Paspalum notatum		do	
		Pennisetum purpureum		Increased forage value and resistance to helminthosporium eye spot	
		Sorghum vulgare var. *sudanense*		Resistance to foliage diseases	
Iowa Ames	H. D. Hughes and F. S. Wilkins	*Phalaris arundinacea*	1921-32	Increased seed and forage, disease resistance, leafiness, and density of turf	Much
Illinois Urbana	O. T. Bonnett	*Agrostis alba*	1934 (continued)	Increased yield of forage, disease resistance, and winter hardiness	
		Poa pratensis	do	Increased yield of forage, resistance to leaf rust and mildew, and winter hardiness	
Kansas Hays [a] (Fort Hays Branch of Kansas Agricultural Experiment Station)	D. A. Savage, H. E. Runyon, and R. E. Solomon	*Agropyron pungens, A. semicostatum, A. smithii*	do	In general the objective for all grasses is to develop drought-resistant grasses suitable for reseeding and resodding on different soil types in the central and southern Great Plains and to improve their forage value	Many promising variants found
		Andropogon furcatus, A. hallii, A. scoparius, Bouteloua gracilis, B. hirsuta	do	Special attention given to increased seed production and viability	
		Buchloe dactyloides	do	Special attention given to increased seed production and viability and rapidity of vegetative spread	
		Bromus inermis	do	Especially to develop a type that will endure high temperatures	
		Elymus virginicus	do	Especially to improve forage quality	
		Sorghastrum nutans	do	Special attention given to increased seed production and viability	
Manhattan [a]	A. E. Aldous	*Andropogon furcatus, A. scoparius*	1928 (continued)	Increased seed and forage values and drought resistance	
		Bromus inermis	1930 (continued)	do	
Kentucky [a] Lexington	F. N. Fergus	*Arrhenatherum elatius*	1931 (continued)	Comparing local strain with commercial	
		Dactylis glomerata	10 years	Increased forage production	
		Festuca elatior	1931 (continued)	Comparing local strain with commercial	
		Poa pratensis	7 years	Increased forage production, disease resistance, and turf density	

Maryland					
Beltsville (National Agricultural Research Center)	H. N. Vinall and M. A. Hein	*Dactylis glomerata*	1932 (continued)	Pasture and hay types, leafiness and late maturing	Medium
		Lolium multiflorum	1930 (continued)	Late maturing and rust resistance	Do
		Lolium perenne	do	Rust resistance and summer forage production	Little
		Poa compressa	1934 (continued)	Leafiness and increased density of turf	Medium
		Poa pratensis	do	Summer forage production	Do
College Park	J. E. Metzger and G. F. Eppley	*Festuca rubra*	5 years	Increased seed production and fine turf value	Do
Michigan					
Augusta* (W. K. Kellogg Demonstration Farm)	A. B. Dorrance	*Cynodon dactylon*	1930–36	Winter hardiness	Do
		Poa pratensis	1934–36	Summer forage production and leafiness	Do
Mississippi					
State College	H. W. Bennett	*Cynodon, Digitaria, Lolium* and *Paspalum* spp.	1936 (continued	Increased seed production and forage value	
Missouri					
Columbia*	E. M. Brown	*Dactylis glomerata*	1935 (continued)	Increased pasturage production and leafiness	
		Poa pratensis	1932 (continued)	Increased pasturage production, drought and heat resistance, dense turf	Medium
Montana					
Bozeman*	L. P. Reitz	*Festuca rubra*	1930–35	Increased seed and forage production	
		Lolium perenne	1930–35	do	
		Sorghum vulgare var. *sudanense*	1930–35	do	
		Various native grasses	1936 (continued)	do	
Havre* (Northern Montana Branch Station)	M. A. Bell	*Agropyron cristatum*	1925	do	Do
		Agropyron inerme	1934	do	
		Agropyron smithii	1934	do	
Moccasin* (Judith Basin Branch Station)	N. F. Woodward, H. E. Tower and J. E. Norton	*Agropyron cristatum*	1924–26, 1929–34, 1935 (continued)	do	Do
Nebraska					
Lincoln*	L. C. Newell, A. L. Frolik and F. D. Keim	*Agropyron cristatum, A. smithii, Andropogon furcatus, A. scoparius, Bouteloua gracilis, B. curtipendula, Bromus inermis, Buchloe dactyloides, Dactylis glomerata, Panicum virgatum, Phalaris arundinacea, Sorghastrum nutans*	1936 (continued)	Increased seed and forage production, drought and disease resistance, palatability, and longevity	
New Jersey					
New Brunswick	H. B. Sprague	*Agrostis canina*	1929 (continued)	Increased seed, resistance to *Pythium* and brown patch and turf quality	Much
		Festuca rubra	1931 (continued)	Increased seed, resistance to *Pythium* and creeping habit	Medium
New York					
Ithaca	D. B. Johnstone-Wallace and C. H. Myers	*Dactylis glomerata*	do	Improved pasture types	Much

TABLE 2.—*Objectives and progress in the selective breeding of grasses as reported by workers in the United States and Canada*—Continued

Location	Individual workers	Genera and species	Period work under way	Objectives	Success attained
UNITED STATES—continued					
North Dakota:					
Dickinson* (substation)	Leroy Moomaw	*Agropyron cristatum*	1928–35	Increased seed and forage production	Medium.
Mandan* (United States Northern Great Plains Field Station).[2]	George A. Rogler	do	1936 (continued)	In general the objectives for all grasses at Mandan are increased seed and forage production, viability of seed, forage palatability, drought and disease resistance, and seedling vigor.	
		Agropyron smithii	do	Rapid spreading of rhizomes, and early foliage emergence.	
		Andropogon furcatus, A. hallii, A. scoparius.	do	Early foliage emergence	
		Bouteloua curtipendula	do	Early foliage emergence and cold resistance	
		Bouteloua gracilis	do	Early foliage emergence	
		Bromus inermis	do		
		Bromus marginatus	do	Cold resistance	
		Buchloë dactyloides	do	Early foliage, dense turf, tall seed stalks, rapid spreading.	
		Elymus canadensis	do		
		Elymus junceus	do	Nonshattering of seed	
		Oryzopsis hymenoides	do		
		Panicum virgatum	do	Early foliage emergence	
		Phalaris arundinacea	do	Nonshattering of seed	
Oklahoma:					
Woodward* (United States Southern Great Plains Field Station).	D. A. Savage, H. E. Runyon, and R. E. Solomon.	*Agropyron repens* var. *pungens, A. smithii, Andropogon furcatus, A. hallii, A. saccharoides, A. scoparius, Bouteloua chondrosioides, B. curtipendula, B. eriopoda, B. hirsuta, Buchloë dactyloides, Calamovilfa longifolia, Elymus virginicus, Panicum virgatum, Redfieldia flexuosa, Sorghastrum nutans, Zoysia japonica.*	do	To develop drought-resistant grasses suitable for reseeding and resodding on different soil types in the central and southern Great Plains and to improve their forage value.	
Stillwater	W. B. Gernert	*Bromus inermis*	Recent years	Increased forage production	
		Buchloë dactyloides	do	do	Much.
		Phalaris arundinacea	do	do	
		Sorghum vulgare var. *sudan-*	do	do	

Oregon:					
Corvallis*	H. A. Schoth and H. H. Rampton.	*Agrostis oregonensis*	1935 (continued)	Improved turf and seed production [3]	Medium.
		Agrostis palustris	do	Deeper root system and ability to withstand brackish overflow.	Do.
		Agrostis sp.	1928 (continued)	Improved forage, turf, and seed production	Do.
		Alopecurus pratensis	1934 (continued)	Increased forage, uniform seed maturity, and less shattering.	Much.
		Arrhenatherum elatius	1932 (continued)	Increased foliage and less seed shattering	Do.
		Brachypodium pinnatum	1928 (continued)	More tender foliage	Little.
		Bromus inermis	1922 (continued)	Reduced rhizome development and early growth.	Medium.
		Dactylis glomerata	1928 (continued)	Improved forage and turf-forming pasture types.	
		Festuca elatior var. *arundinacea*.	1920 (continued)	More tender foliage and less seed shattering	Do.
		Lolium multiflorum	1930 (continued)	Longevity and rust resistance	Do.
		Lolium perenne	do	Longevity, rust resistance, and more seed first year.	Do.
		Phalaris arundinacea	1920 (continued)	Wider adaptation as to soil and increased seed production; especially less shattering.	Much.
		Phalaris tuberosa var. *stenoptera*.	1930 (continued)	Longevity, less seed shattering, and winter hardiness.	
Pennsylvania:					
State College	H. B. Musser	*Agrostis canina*	1929–35	Fine turf	Do.
		Agrostis palustris	1929–35	do	Medium.
		Poa pratensis	1932 (continued)	Improvement in pasture value and fine-turf quality.	Do.
Rhode Island:					
Kingston	T. E. Odland and H. F. A. North.	*Agrostis alba*	1930–34	Purifying lines	Much.
		Agrostis canina	1931–35	(a) Purifying lines, (b) resistance to dollar spot, seed production, fine turf.	Do.
		Agrostis palustris	1930–34	Resistance to brown patch, dollar spot, and snow mold; and fine turf.	Medium.
		Agrostis tenuis	1930 (continued)	(a) Resistance to brown patch, (b) fine turf, (c) purifying lines.	(c) Much.
Texas:					
San Antonio [2]	Gerald O. Mott	*Andropogon furcatus*, *A. hallii*, *A. saccharoides*, *A. scoparius*, *Bouteloua curtipendula*, *B. gracilis*, *B. hirsuta*, *Panicum virgatum*, *Sorghastrum nutans*.	1934 (continued)	Increased production and viability of seed, forage value, longevity, and drought resistance.	
Spur (Texas Substation no. 7).	R. E Dickson	*Buchloë dactyloides*	Few years	Selection and increased yields of forage and seed.	Much.

[2] Bureau of Plant Industry and Soil Conservation Service cooperating.
[3] In addition to objectives stated, general consideration is given in all species at Corvallis to increasing the quantity and quality of forage and resistance to insects and diseases.

Table 2.—*Objectives and progress in the selective breeding of grasses as reported by workers in the United States and Canada*—Continued

Location	Individual workers	Genera and species	Period work under way	Objectives	Success attained
UNITED STATES—continued					
Utah					
Logan*	Wesley Keller and Dean F McAlister	*Agropyron cristatum A pauciflorum, A smithii, Bromus inermis Elymus canadensis E condensatus, Festuca idahoensis, Oryzopsis hymenoides, Poa bulbosa P nevadensis, Sporobolus airoides Stipa comata*	1936 (continued)	All species are selected for increased forage production drought resistance, palatability, and a greater capacity for survival and reproduction under moderately heavy grazing	
Virginia					
Arlington (Arlington Experiment Farm, U S Department of Agriculture)	Staff of U S Golf Association, Green Section	*Agrostis canina*	1920 (continued)	Dense turf uniform texture, and resistance to diseases, trampling, and close clipping	Do
		Agrostis palustris	do	do	Do
		Festuca rubra	1931 (continued)	Dense turf uniform texture and resistance to diseases rapid spread, and close clipping	Little
		Poa pratensis	do	Dense turf uniform texture, and resistance to disease, drought and close clipping	Do
		Poa trivialis	do	Dense turf and resistance to diseases and trampling	Medium
Blacksburg	T K Wolfe and N A Pettinger	*Dactylis glomerata*	1920–36	Increased forage value	Much
Washington					
Pullman	A L Hafenrichter and V B Hawk	*Agropyron cristatum A pauciflorum*	1935 (continued)	Increased seed and forage production	Little
Pullman*	D C Smith and G W Fischer	*Agropyron cristatum*	1936 (continued)	Sustained seed yields, increased palatability and resistance to smut	
		Agropyron inerme	do	Leafiness and improved seeding habits	
		Agropyron pauciflorum	do	Resistance to drought and diseases	
		Arrhenatherum elatius	do	Increased palatability and leafiness, improved seeding habits, and smut resistance	
		Bromus inermis	do	Drought resistance and improved seed production	
		Bromus marginatus	do	Smoothness of foliage and smut resistance	
		Dactylis glomerata	do	Drought and cold resistance and improved seed production	
		Elymus canadensis	do	Obtaining awnless and finer stemmed types	
		Festuca elatior	do	Increased palatability and better seeding habits	
		Phalaris arundinacea	do	Drought resistance, winter hardiness and seed production	
Wisconsin					
Madison*	O S Aamodt, F W Tinney, and H L Ahlgren	*Bromus inermis*	1935 (continued)	Increased forage production, resistance to leaf spot, and reduced rhizomes	Medium to much
		Dactylis glomerata	1936 (continued)	Increased forage production with longer vegetative period and drought resistance	

		Poa pratensis	do	Increased forage production resistance to mildew and drought resistance	
Wyoming					
Cheyenne (Cheyenne Horticultural Field Station U S Department of Agriculture)	H M Benedict	*Agropyron cristatum*	do	( )	
		Agropyron pauciflorum	do	Emphasis on longevity	
		Agropyron smithii	do		
		Agropyron spicatum	do		
		Bouteloua curtipendula	do		
		Bouteloua gracilis	do		
		Bromus inermis	do	Reduced rhizome development	
		Bromus marginatus	do		
		Buchloe dactyloides	do		
		Elymus condensatus	do	Emphasis on palatability	
		Stipa comata	do	Reduced awn development	
Hawaii					
Honolulu	C P Wilsie	*Bromus catharticus*	1934 (continued)	Increased forage and seed production and resistance to smut	
		Digitaria milanjiana D pentzii	1935 (continued)	Increased pasturage development of uniform pasture type	
		Pennisetum purpureum	1933 (continued)	Increased forage leafiness and palatability	
		Sorghum vulgare var sudanense	1933 34	Increased forage, leafiness, and resistance to smut	
CANADA					
Alberta					
Edmonton (University of Alberta)	M O Malte and G H Cutler	*Agropyron pauciflorum*	Several years	Improved hay type	Medium
Ontario					
Guelph (Ontario Agricultural College)	O McConkey	*Agropyron cristatum*	7 years	Increased seed production, forage yield, and (a) leafiness	(a) Much
		Agrostis alba	10 years	Increased seed production, disease resistance, pasturage (a) leafiness, and (b) winter hardiness	(a) and (b) Medium
		Bromus inermis	4 years	Increased seed production, disease resistance, pasturage, and (a) leafiness	(a) Medium
		Dactylis glomerata	10 years	Pasture and pasture hay type winter hardiness, and leafiness	Much
		Festuca elatior	10 years	Increased seed production, disease resistance, forage production, (a) leafiness, and (b) winter hardiness	(a) and (b) Much
		Festuca rubra	6 years	Increased seed production, disease resistance, and turf and pasture value	Medium
		Lolium perenne	10 years	Increased seed and forage, disease resistance, and winter hardiness	Medium hardiness
		Phalaris arundinacea	6 years	Increased seed, disease resistance, pasture value leafiness	Medium
		Poa compressa	10 years	Same also winter hardiness	Much
		P pratensis	10 years	do	Medium

[4] The objectives listed for Washington are the ones to be emphasized in each instance In general the objectives for all species are increased seed and forage yields, greater palatability, and resistance to drought, heat, and disease

[5] All species at Cheyenne are being selected for increased early growth, seed production, winter hardiness, palatability, longevity, and drought and disease resistance Additional or special objectives are indicated

TABLE 2.—*Objectives and progress in the selective breeding of grasses as reported by workers in the United States and Canada*—Continued

Location	Individual workers	Genera and species	Period work under way	Objectives	Success attained
CANADA—continued					
Ottawa (Central Experimental Farm).	L. E. Kirk and R. McVicar.	*Agropyron pauciflorum*	1913–29	Increased forage production, uniformity, fineness and abundance of leaves.	Much.
		Dactylis glomerata	1912 (continued)	Winter hardiness	Do.
		Festuca elatior	1918 (continued)	(a) Increased forage production, (b) uniformity in type suitable for hay and pasture.	(a) Little, (b) medium.
		Poa pratensis	1919 (continued)	(a) Increased forage production, (b) mildew resistance, (c) upright habit of growth, and also spreading habit of growth.	(a) Unestimated, (b) much, (c) much.
Quebec:					
Quebec (Macdonald College).	L. S. Klinck, L. A. Waitzinger, G. P. McRostie, A. MacTaggart, and J. N. Bird.	*Dactylis glomerata*	1911–33	Increased hay and aftermath, winter hardiness, and longevity.	Medium.
Saskatchewan	L. E. Kirk and T. M. Stevenson.	*Agropyron cristatum*	1915 (continued)	Increased hay and pasturage	Much.
Saskatoon (Dominion Forage Crops Laboratory).	L. E. Kirk	*Agropyron pauciflorum*	1922–29	Increased hay	Medium.
	T. M. Stevenson and W. J. White.	do	1933 (continued)	Longevity	
	J. Bracken	*Bromus inermis*	?–1921	Increased hay and pasture	Medium.
	L. E. Kirk and T. M. Stevenson.	do	1923 (continued)	Increased hay and pasture, reduced rhizome development, leafiness, and fineness of stem.	Much.

TABLE 3 — *Nature and characteristics of interspecific hybrids previously reported*

Parents of cross and chromosome numbers (2n)	By whom made	Institution	Date of cross	Characteristics of progeny
Dactylis glomerata 28 × *D aschersoniana* 14	Muntzing (20)	Swedish Seed Association Seed Control Laboratory Svalof Sweden	1931 35	The F_1 chromosome number was 21 the male sterile and female partially sterile when backcrossed on the *D glomerata* produced well developed plants that were self fertile more vigorous than the *D glomerata*, and had ± 35 chromosomes
Festuca arundinacea 42 × *F gigantea* 42	Nilsson (22)	Swedish Seed Association Seed Control Laboratory Undrom Sweden	1934	Chromosome number of the F_1 was 42, but F_1 progeny plants differed very much, one having a chromosome number of 84
Do	Jenkin (14)	Welsh Plant Breeding Station Aberystwyth Wales	1930	F_1 sterile pollen not liberated but in many cases the F_1 plants can be used as female parents for backcrossing some more readily than others
F pratensis 14 × *F arundinacea* 42	Nilsson Leissner	Swedish Seed Association		Cross reported successful, but no description of progeny was given
Do	Jenkin (13)[1]	Welsh Plant Breeding Station Aberystwyth Wales	1924 1928	F_1 sterile pollen not liberated but in many cases the F_1 plants can be used as female parents for backcrossing some more readily than others
F pratensis 14 × *F gigantea* 42	do	do	1930	Do
F pratensis 14 × *F rubra* 42	do	do	1922 1928 1930 1931	10 percent of pollinated flowers produced seeds but none of these germinated
F rubra 42 × *F ovina* 14	do	do	1930	F_1 sterile pollination very incomplete but in many cases the F_1 plants can be used as female parents for backcrossing, some more readily than others
Lolium perenne 14 × *L multiflorum* 14	Woodforde (29)	Department of Agriculture Tasmania Australia		The F_2 segregated in a ratio of 3 4 1 for seedling fluorescence a characteristic of *L multiflorum* Italian characters were dominant No genetic linkage between fluorescence and awned glumes
Do -	Jenkin[1]	Welsh Plant Breeding Station Aberystwyth Wales	Various	F_1 fertile provisional conclusion that better results by selecting within either *L perenne* or *L multiflorum* than from the hybrid progeny
L perenne 14 × *L remotum*	do	do	do	F_1 sterile pollen not liberated but in many cases the F_1 plants can be used as female parents for backcrossing, some more readily than others
L perenne 14 × *L rigidum*	Jenkin (14)	do	do	F_1 fertile, but no description of progeny given

[1] Reported in correspondence (Y B Q)

TABLE 3.—*Nature and characteristics of interspecific hybrids previously reported*—Continued

Parents of cross and chromosome numbers (2*n*)	By whom made	Institution	Date of cross	Characteristics of progeny
L perenne 14 × *L temulentum* 14	Jenkin [1]	Welsh Plant Breeding Station Aberystwyth Wales	1922	F_1 sterile pollen not liberated but in many cases the F_1 plants can be used as female parents for backcrossing some more readily than others F_1 of reciprocal cross similar in all essential characters
L temulentum 14 × *L oliaceum* (?)	do	do	1935	Cross reported successful, but characteristics of F_1 unknown
L temulentum 14 × *L remotum* (?)	do	do	1935	Do
Phalaris arundinacea 28 × *P tuberosa* 28	Jenkin (*16*)	do	1930	Chromosome number of F_1, 28, of which 12 are bivalent and 2 univalent The hybrids are very vigorous and easily distinguishable from the parent species
Poa arachnifera ±80 × *P pratensis* 56	E Marion Brown [1]	U S Department of Agriculture and Missouri Agricultural Experiment Station, Columbia Mo	1934 35	About 10 percent of the F_1 hybrids are fertile, progeny of these are productive have more vigorous rhizomes and show greater resistance to heat and drought than *P pratensis*
P pratensis 56 × *P alpina* 32–34	Muntzing [1]	Swedish Seed Association, Svalof Sweden		Cross reported successful, but no description of the progeny given
Sorghum vulgare 20 × *S halepense* 40	Karper and Chisholm (*16*)	Texas Agricultural Experiment Station, College Station, Tex		Chromosome numbers of F_1, 30 an examination of the pollen mother cells of F_1 plant showed univalents bivalents, trivalents, and quadrivalents but none of higher association
S vulgare var *sudanense* 20 × *S halepense* 40	Karper (*2*)		1933	Small percentage of success F_1 partially sterile

[1] Reported in correspondence (Y B Q)

TABLE 4.—*Intergeneric hybrids previously reported*

Parents of cross and somatic chromosome numbers	By whom made	Institution	Date made or reported	Remarks
Aegilops cylindrica 28 × *Agropyron elongatum* 70.	W. J. Sando [1]	U. S. Department of Agriculture, Bureau of Plant Industry, Washington, D. C.	1935	42 flowers pollinated; 3 seeds obtained, all of which produced plants.
Aegilops longissima 14 × *Agropyron elongatum* 70.	do	do	1935	48 flowers pollinated; 18 seeds obtained, none of which grew.
Aegilops speltoides 14 × *Agropyron elongatum* 70.	do	do	1935	106 flowers pollinated; 2 seeds obtained, none of which produced plants.
Aegilops crassa 42 × *Agropyron intermedium* 42.	Verushkin [1]	Central Station of Plant Breeding and Genetics, Saratov, Union of Soviet Socialist Republics.	1935	46 flowers pollinated; 29 seeds obtained, 63 percent pollinations successful.
Aegilops speltoides 14 × *Agropyron intermedium* 42.	do	do	1935	28 flowers pollinated; 8 seeds obtained, 28.5 percent pollinations successful.
Aegilops triaristata 28 or 42 × *Agropyron intermedium* 42.	do	do	1935	6 flowers pollinated; 3 seeds obtained, 50 percent pollinations successful.
Aegilops triuncialis 28 × *Agropyron intermedium* 42.	do	do	1935	12 flowers pollinated; 2 seeds obtained, 16.6 percent pollinations successful.
Aegilops turcomanica 42 × *Agropyron intermedium* 42.	do	do	1936	18 flowers pollinated; 10 seeds obtained, 55.5 percent pollinations successful.
Aegilops variabilis 28 × *Agropyron intermedium* 42.	do	do	1935	22 flowers pollinated; 6 seeds obtained, 27.3 percent pollinations successful.
Festuca arundinacea 42 × *Lolium perenne* 14.	Jenkin (*13*) [1]	Welsh Plant Breeding Station, Aberystwyth, Wales.	1921, 1928–30	429 flowers pollinated; 26.8 percent set seed, but none germinated.
F. pratensis 14 × *L. perenne* 14	do	do	1922, 1928–31	1,513 flowers pollinated; 27 percent set seed; 4.9 percent germinated; 7 plants established F_1 male sterile.
F. rubra 42 or 56 × *L. perenne* 14	do	do	1921, 1922, 1928	181 flowers pollinated; 13 seeds obtained; 7.2 percent set seed, but none germinated.
Lolium perenne 14 × *F. arundinacea* 42	do	do	1921, 1928, 1929, 1931	654 flowers pollinated; 32.9 percent set seeds 39.5 percent germinated; 75 plants established, F_1 sterile.
L. perenne 14 × *F. gigantea* 28	do	do	1921	Successful in obtaining seed, but F_1 sterile.
do	F. Nilsson [1]	Swedish Seed Association, Svalof, Sweden.		Cross reported successful, but no description given.
L. perenne 14 × *F. ovina* 28	Jenkin (*13*) [1]	Welsh Plant Breeding Station, Aberystwyth, Wales.	1930	150 flowers pollinated; 16.7 percent set seed; none of which germinated.
L. perenne 14 × *F. pratensis* 14	do	do	1922, 1928–31	2,046 flowers pollinated; 41.1 percent set seed, germination 0.7 percent; 1 plant established; F_1 sterile.
do	F. Nilsson [1]	Swedish Seed Association, Svalöf, Sweden.		Cross reported successful, but no description given.
L. perenne 14 × *F. rubra* 42	Jenkin (*13*)	Welsh Plant Breeding Station, Aberystwyth, Wales.	1921, 1924, 1928	218 flowers pollinated; 45.4 percent set seed; germination 18.2 percent; 9 plants established; F_1 sterile.

[1] Reported in reply to the Yearbook questionnaire, 1936.

TABLE 4.—*Intergeneric hybrids previously reported*—Continued

Parents of cross and somatic chromosome numbers	By whom made	Institution	Date made or reported	Remarks
L. perenne 14 × *F. rubra* 42	F. Nilsson and G. Nilsson Leissner[1]	Swedish Seed Association, Svalof, Sweden		Cross reported successful but no description given
Triticum dicoccoides 28 × *Agropyron elongatum* 70	W. J. Sando[1]	U. S. Department of Agriculture, Bureau of Plant Industry, Washington, D. C.	1935	96 flowers pollinated, 7 seeds obtained, 4 seeds planted, 2 percent of which produced plants.
T. spelta 42 × *A. elongatum* 70	do	do	1935	54 flowers pollinated, 9 seeds obtained, 7 seeds planted, 6 percent of which produced plants
T. aestivum 42 × *A. elongatum* 70	do	do	1935	2,128 flowers pollinated, 398 seeds obtained, 140 seeds planted, 10.5 percent of which produced plants
T. dicoccum 28 × *A. glaucum* 42	L. E. Kirk and R. McVicar[1]	Central Experimental Farm, Ottawa, Canada	1935	Cross successful. F_1 hybrids male sterile, may be backcrossed on *Triticum* parent
T. durum 28 × *A. glaucum* 42	do	do	1935	Do
T. aestivum 42 × *A. glaucum* 42	do	do	1935	Do
T. dicoccum 28 × *A. elongatum* 70	do	do	1935	Do
T. durum 28 × *A. elongatum* 70	do	do	1935	Do
T. aestivum 42 × *A. elongatum* 70	do	do	1935	Cross successful. F_1 hybrids showed partial fertility
T. durum 28 × *A. elongatum* 70	T. M. Stevenson and W. J. White[1]	Dominion Forage Crops Laboratory, Saskatoon, Saskatchewan, Canada	1935	Cross reported successful but fertility of F_1 not yet determined
T. polonicum 28 × *A. elongatum* 70	do	do	1935	Do
T. aestivum 42 × *A. elongatum* 70	do	do	1935	Do
T. durum 28 × *A. glaucum* 42	do	do	1935	Do
T. polonicum 28 × *A. glaucum* 42	do	do	1935	Do
T. aestivum 42 × *A. glaucum* 42	do	do	1935	Do
T. dicoccum 28 × *A. glaucum* 42	Armstrong (*1*)	Central Experimental Farm, Ottawa, Canada	1935–36	1,196 flowers pollinated, 1,414 seeds obtained, 34.6 percent successful
T. dicoccum 28 × *A. elongatum* no. 820, 70	do	do	1935–36	1,391 flowers pollinated, 538 seeds obtained, 38.7 percent successful
T. dicoccum 28 × *A. elongatum* no. 1083, 70	do	do	1935–36	196 flowers pollinated, 3 seeds obtained, 1.5 percent successful
T. durum 28 × *A. glaucum* 42	do	do	1935–36	1,224 flowers pollinated, 394 seeds obtained, 32.2 percent successful
T. durum 28 × *A. elongatum* no. 820, 70	do	do	1935–36	345 flowers pollinated, 11 seeds obtained, 3.2 percent successful
T. durum 28 × *A. elongatum* no. 1083, 70	do	do	1935–36	164 flowers pollinated, 12 seeds obtained, 7.3 percent successful
T. aestivum 42 × *A. glaucum* 42	do	do	1935–36	1,041 flowers pollinated, 122 seeds obtained, 11.7 percent successful
T. aestivum 42 × *A. elongatum* no. 820, 70	do	do	1935–36	239 flowers pollinated, 25 seeds obtained, 10.5 percent successful
T. aestivum (Kharkov) 42 × *A. elongatum* no. 1083, 70	do	do	1935–36	328 flowers pollinated, 45 seeds obtained, 13.7 percent successful

T durum 28 × *A elongatum* 70	Vakar (34)	Siberian Institute for Scientific Research of Grain Management, Union of Soviet Socialist Republics Omsk		Success with cross, 49 somatic chromosomes in the F_1 hybrid
T aestivum 42 × *A elongatum* 70	do	do		Success with cross, 56 somatic chromosomes in the F_1 hybrid
T aestivum × *A glaucum* 42	do	do		Success with cross 42 somatic chromosomes in the F_1 hybrid
T aestivum 42 × *A intermedium* 42	Verushkin (35)	Central Station of Plant Breeding and Genetics Saratov Union of Soviet Socialist Republics	1935	3 062 flowers pollinated 1 248 seeds obtained, 40 7 percent successful
T sphaerococcum 42 × *A intermedium* 42	do	do	1935	80 flowers pollinated 24 seeds obtained, 30 percent successful
T compactum 42 × *A intermedium* 42	do	do	1935	80 flowers pollinated, 10 seeds obtained 12 5 percent successful
T dicoccoides 28 × *A intermedium* 42	do	do	1935	180 flowers pollinated, 52 seeds obtained 28 8 percent successful
T dicoccum 28 × *A intermedium* 42	do	do	1935	128 flowers pollinated, 39 seeds obtained, 30 5 percent successful
T durum 28 × *A intermedium* 42	do	do	1935	1 207 flowers pollinated 564 seeds obtained, 46 7 percent successful
T polonicum 28 × *A intermedium* 42	do	do	1935	48 flowers pollinated, 21 seeds obtained 43 7 percent successful
T persicum 28 × *A intermedium* 42	do	do	1935	256 flowers pollinated 131 seeds obtained, 51 2 percent successful
T monococcum 14 × *A intermedium* 42	do	do	1935	86 flowers pollinated, 14 seeds obtained, 16 3 percent successful
T aestivum 42 × *A elongatum* 70	do	do	1935	2 136 flowers pollinated 937 seeds obtained, 43 8 percent successful
T sphaerococcum 42 × *A elongatum* 70	do	do	1935	59 flowers pollinated, 31 seeds obtained, 52 5 percent successful
T compactum 42 × *A elongatum* 70	do	do	1935	18 flowers pollinated 3 seeds obtained, 16 6 percent successful
T dicoccoides 28 × *A elongatum* 70	do	do	1935	54 flowers pollinated 22 seeds obtained, 40 7 percent successful
T dicoccum 28 × *A elongatum* 70	do	do	1935	328 flowers pollinated 93 seeds obtained 28 5 percent successful
T durum 28 × *A elongatum* 70	do	do	1935	1 128 flowers pollinated 469 seeds obtained, 41 5 percent successful
T turgidum 28 × *A elongatum* 70	do	do	1935	24 flowers pollinated, 10 seeds obtained, 41 5 percent successful
T persicum 28 × *A elongatum* 70	do	do	1935	70 flowers pollinated 26 seeds obtained, 37 1 percent successful
T monococcum 14 × *A elongatum* 70	do	do	1935	24 flowers pollinated, 0 seeds obtained 0 0 percent successful

[1] Reported in reply to the Yearbook questionnaire, 1936

TABLE 5.—*Chromosome numbers of various grasses*

Genus and species [1]	Somatic chromosome number (2*n*) [2]	Reference [3]
Aeluropus littoralis var. *dasyphylla* Trautv.†	20	(5)
A. littoralis (Gouan) Parl.†	60	(5)
Agropyron acutum (DC.) Roem. and Schult	35	(46)
A. aegilopoides Drobov	14	(4)
A. caninum (L.) Beauv	28 a	(42)
A. ciliare (Trin.) Franch	28	(39)
A. cristatum (L.) Gaertn	28 c	(41)
A. cristatum (Fairway strain)	14*	([4])
A. dagnae Grossh	14 a	(42)
A. dasystachyum (Hook.) Scribn	28	(42)
A. desertorum (Fisch.) Schult.†	28	(42)
A. elongatum (Host) Beauv.†	70	(42)
A. glaucum (DC.) Roem. and Schult	42	(42)
A. griffithsii Scribn. and Smith	28	(42)
A. intermedium (Host) Beauv. (See *A. obtusiusculum*.)		
A. japonicum Honda.=*A. japonense* Honda	28	(39)
A. junceum (L.) Beauv	28 a	(42)
A. mutabile Drobov	28	(4)
A. obtusiusculum Lange=*A. intermedium*	42	(42)
A. orientale (L.) Roem. and Schult	28	(3)
A. pauciflorum (Schwein.) Hitchc	28 a	(42)
A. prostratum (Pall.) Beauv	14	(4)
A. pungens (Pers.) Roem. and Schult	42* a	(42)
A. repens (L.) Beauv	42 b	(42)
Do	28	(4)
A. richardsoni Schrad.=*A. subsecundum*	28	(41)
A. semicostatum (Steud.) Nees	42	(39)
A. sibiricum (Willd.) Beauv.†	28 b	(3)
A. smithii Rydb	56 a	(42)
A. smithii var. *molle* (Scribn. and Smith) Jones	28, 56	(42)
A. spicatum (Pursh) Scribn. and Smith	14	(42)
A. subsecundum (Link) Hitchc. (See *A. richardsoni*.)		
A. tunguscense Drobov	28	(4)
A. villosum (L.) Link	14*	(42)
Agrostis alba L	42 a	(3)
A. nebulosa Bois. and Reut	14 a	(4)
A. tenuis Sibth. (See *A. vulgaris*.)		
A. verticillata Vill	28	(4)
A. vulgaris With.=*A. tenuis*	28	(3)
A. spica-venti L. (See *Apera spica-venti*.)		
Alopecurus aequalis Sobol. (See *A. fulvus*.)		
A. agrestis L.=*A. myosuroides*	14 a	(3)
A. alpinus J. E. Smith. var. *elatus* Kom	70	(4)
A. fulvus J. E. Smith†=*A. aequalis*	14	(24)
A. geniculatus L	28 a	(3)
A. myosuroides Huds. (See *A. agrestis*.)		
A. pratensis L	28 d	(3)
Ammophila breviligulata Fernald	28*	(9)
Andropogon annulatus Forsk.†	40*	(23)
A. condylotrichus Hochst. (See *A. piptatherus*.)		
A. elliottii Chapm	20	(19)
A. furcatus Muhl	70*	(10)
A. gryllus L.=*Rhaphis gryllus*	40	(4)
A. halepensis (L.) Brot. (See also *Sorghum halepense*)	40 f	(3)
A. halepensis var	20	(24)
A. intermedius R. Br	[5] 70	(3)
A. nardus L.=*Cymbopogon nardus*.	20	(27)
A. piptatherus Hack.=*A. condylotrichus*	40	(1)
A. purpureo-sericeus Hochst.†=*Sorghum purpureo-sericeum*	40	(33)
A. saccharoides Swartz	60	(4)
A. scoparius Michx	40 a	(10)
A. sorghum (L.) Brot.=*Sorghum vulgare*	20 e	(28)
A. sorghum Brot. var. *sudanense* Piper=*Sorghum vulgare* var. *sudanense*	20 a	(14)
A. versicolor=*Sorghum versicolor*	10 a	(22)
Anthephora hermaphrodita (L.) Kuntze	18	(3)
Anthoxanthum aristatum Boiss	10	(3)
A. odoratum L	20 b	(3)
Apera spica-venti (L.) Beauv.=*Agrostis spica-venti*	14	(4)
Apluda mutica L	40 a	(3)
A. mutica L	20	(19)
Aristida adscensionis L	22	(5)
Arrhenatherum elatius (L.) Mert. and Koch	28* c	(2)
Arthraxon ciliaris Beauv. subsp. *langsdorfii* (Trin.) Hack	40	(3)
A. hispidus (Thunb.) Makino	40	(3)
Arundinaria fortunei (Van Houtte) Riviere†	48	(19)
A. glaucescens (Willd.) Beauv	70–74	(3)
A. hindsii Munro	48	(52)
A. pygmaea Kurz	54	(19)
Arundinella anomala Steud	36	(4)
Arundo donax L	100+a	(4)
Asprella hystrix Willd.†=*Hystrix patula*	28	(3)
Atropis distans (L.) Griseb.=*Puccinellia distans*	42	(4)
A. distans (L.) Griseb	28	(47, 48)
Do	14	(4)
Avena algeriensis Trabut	42	(25)
A. barbata Brot.†	28 d	(25)
A. bruhnsiana Gruner	14	(12)
A. brevis Roth†	14 b	(10)
A. byzantina C. Koch†	42 a	(25)
A. clauda Dur	14 a	(40)
A. fatua L	42 a	(25)
A. flavescens L.=*Trisetum flavescens*	28	(37)
A. ludoviciana Dur.†	42	(20)

[1] Authorities for the botanical names used have been corrected to agree with the International Code and the U. S. Department of Agriculture style. Those names for which no authority was given in the original are indicated by a dagger (†) and the recognized authority for the name has been inserted, but this does not mean that the grasses were correctly identified by the cytologist.

[2] Letters following chromosome numbers denote the number of times this number has been verified by other authors than the one indicated by the reference in the last column. a=1, b=2, c=3, d=4, e=5, f=6, g=7. An asterisk (*) indicates those reported as the "*n*" number, the number here given being double that reported.

[3] Numbers in parentheses refer to References for Chromosome Numbers, p. 1099. Where a number has been verified by several workers, only the first report of that number is cited.

[4] W. N. Myers, personal correspondence.

[5] About.

Table 5.—*Chromosome numbers of various grasses*—Continued

Genus and species	Somatic chromosome number (2*n*)	Reference
A. nuda L.	42	(20)
A. sativa L.	42 a	(25)
A. sterilis L.	42 e	(20)
A. strigosa Schreb.† subsp. *abyssinica* (Hochst.) Hausskn.†	28	(12)
A. strigosa Schreb.	14 e	(25)
A. wiestii Steud.†	14 c	(20)
Beckmannia erucaeformis (L.) Host.	14	(4)
Boissiera bromoides Hochst. and Steud.†	28	(47, 48)
B. pumilio (Trin.) Stapf.	14	(4)
Bouteloua gracilis (H. B. K.) Lag.†	42	([6])
B. oligostachya (Nutt.) Torr.= *Bouteloua gracilis*	40	(4)
Brachiaria erucaeformis (J. E. Smith) Griseb. (See *Panicum erucaeforme*.)		
B. mutica (Forsk.) Stapf	36	(19)
Brachypodium distachyon (L.) Beauv. (See *Trachynia distachya*.)		
B pinnatum (L.) Beauv.†	28	(24)
B. sylvaticum (Huds.) Beauv	18	(3)
Briza elatior S. Smith.	14–17	(4)
B. maxima L.	14 a	(3)
B. media L	14 a	(3)
B. minor L.	10 a	(3)
Bromus abolinii Drobov	14	(4)
B. albidus Bieb.	28	(4)
B. arduennensis Dum	14	(47, 48)
B. arvensis L.	14 a	(3)
B. australis R. Br.†	28	(47, 48)
B. breviaristatus Buckl.	56	(47, 48)
B. brizaeformis Fisch. and Mey	14	(3)
B. cappadocicus Boiss. and Bal.	42	(47, 48)
B. carinatus Hook. and Arn.	56 a	(47, 48)
B. carinatus var. *hookerianus* (Thurb.) Shear.	14	(47, 48)
B. cartharticus Vahl. (See *B. unioloides*.)		
B. ciliatus L.	56	(4)
B. ciliatus L	14	(47, 48)
B. erectus Huds	42	(47, 48)
B. erectus Huds. subsp. *eu-erectus* Aschers. and Graeb	56* a	(24)
B. inermis Leyss	56	(3)
B. inermis Leyss	42 a	(47, 48)
B. intermedius Guss.	14	(3)
B. japonicus Thunb.	14 a	(3)
B. kalmii A. Gray	14	(47, 48)
B. macrostachys Desf.	28	(3)
Do.	14	(47, 48)
B. madritensis L.	28	(4)
Do	42	(47, 48)
B. marginatus Nees	56 a	(4)
B. mollis L.	28 a	(3)
B. pacificus Shear	42	(47, 48)
B. polyanthus Scribn	42	(47, 48)
B. pumpellianus Scribn.	42	(47, 48)
B. purpurascens Del.=*B. rubens*	28 a	(47, 48)
B. ramosus Huds.	14	(47, 48)
B. rigidus Roth. (See *B. villosus*).		
B. rigidus var. *gussonii*. (See *B. villosus* var. *gussonii*.)		
B. rubens L. (See *B. purpurascens*.)		
B. secalinus L.	28 a	(3)
B. sitchensis Trin.†	42	(47, 48)
B. squarrosus L.	14	(47, 48)
B. sterilis L.	14	(47, 48)
B. tectorum L.	14 a	(3)
B. unioloides H. B. K.=*B. catharticus*	28 a	(47, 48)
B. variegatus Bieb	42	(47, 48)
B. villosus Forsk.†=*B. rigidus*	42 a	(3)
B. villosus var. *gussonii* Aschers. and Graebn.†=*B. rigidus* var. *gussonii*	28	(47, 48)
B. virens Buckl.=*B. carinatus*	14	(47, 48)
Buchloë dactyloides (Nutt.) Engelm.	60	(4)
Calamagrostis arundinacea (L.) Roth	28	(4)
C. epigeios (L.) Roth	[5] 70	(4)
C. neglecta (Ehrh.) Gaertn.†	[5] 70	(4)
Catabrosa aquatica (L.) Beauv	21 (?) a	(47, 48)
Cenchrus barbatus Schum. (See *C. catharticus*.)		
C. brownii Roem. and Schult. (See *C. inflexus*.)		
C. catharticus Del.†=*C. barbatus*	34	(3)
C. echinatus L	34	(3)
C. inflexus R. Br. =*C. brownii*	34	(3)
C. myosuroides H. B. K	[5] 70	(3)
C. tribuloides L	34 a	(3)
Centotheca latifolia (Osbeck) Trin	24	(4)
Chaeturus fasciculatus Link	14	(3)
Chloris acuminata Trin.=*C. distichophylla*	40	(3)
C. barbata (L.) Swartz=*C. inflata*	20	(3)
C. cucullata Bisch	40	(3)
C. distichophylla Lag. (See *C. acuminata*.)		
C. gayana Kunth	20 a	(3)
C. inflata Link. (See *C. barbata*.)		
C. submutica H. B. K	80	(4)
C. truncata R. Br.	40	(3)
Cinna arundinacea L	40	(3)
Cleistogenes serotina (L.) Keng. (See *Diplachne serotina*.)		
Coix lacryma-jobi L	20 a	(4)
Cornucopiae cucullatum L	14	(3)
Cortaderia argentea (Nees) Stapf.= *C. selloana*	70 a	(26)
C. selloana (Schult.) Aschers. and Graebn. (See *C. argentea* and *Gynerium argenteum*.)		
Corynephorus canescens (L.) Beauv.	14	(4)
Cymbopogon nardus (L.) Rendle. (See *Andropogon nardus*.)		
Cynodon dactylon (L.) Pers	36	(3)
C. dactylon (L.) Pers	30	(19)
Cynosurus balansae Coss. and Dur.	14	(3)
C. cristatus L	14 a	(3)
C. echinatus L	14 a	(3)
Dactylis aschersoniana Graebn.†	14* b	(24)
D. glomerata L	28 d	(11)
Dactyloctenium aegyptium (L.) Richt.†	48	(3)
Deschampsia caespitosa (L.) Beauv.	28	(3)
Desmazeria sicula (Jacq.) Dum	14 b	(3)
Digitaria exilis (Kipp.) Stapf	54	(19)
D. sanguinalis (L.) Scop.	28*	(10)
D. horizontalis Willd.†	36	(3)
Dinebra retroflexa (Vahl) Panz	20	(3)
Diplachne serotina (L.) Link†= *Cleistogenes serotina*	40	(4)
Echinaria capitata (L.) Desf	18	(4)
Echinochloa crusgalli (L.) Beauv	42*	(10)
E. crusgalli (L.) Beauv. var. *edulis* Hitchc. = *E. crusgalli* var. *frumentacea*	56*	(10)

[5] About.
[6] L. M. Humphrey; personal correspondence.

TABLE 5.—*Chromosome numbers of various grasses*—Continued

Genus and species	Somatic chromosome number (2*n*)	Reference
E. crusgalli var. *frumentacea* (Roxb.) Wight. (See *E. crusgalli* var. *edulis*.)		
E. frumentacea (Roxb.) Link = *E. crusgalli* var. *frumentacea*	36	(19)
Ehrharta panicea Sm	24*	(4)
Eleusine coracana (L.) Gaertn	36 b	(3)
E. indica (L.) Gaertn	18	(4)
E. tristachya (Lam.)	18	(3)
Elymus canadensis L	28 a	(3)
E. caput-medusae L. (See *Hordeum caput-medusae*.)		
E. curvatus Piper = *E. virginicus* var. *submuticus*	28	(4)
E. dahuricus Turcz	42	(3)
E. giganteus Vahl	28	(4)
E. sibiricus L	28 a	(3)
E. virginicus var. *submuticus* Hook. (See *E. curvatus*.)		
Eragrostis abyssinica (Jacq.) Link.†	40	(3)
E. albida Hitchc	40	(18)
E. aspera (Jacq.) Nels	20	(4)
E. cambessediana (Kunth) Steud	20	(18)
E. capensis (Thunb.) Trin	40	(3)
E. ciliamensis (All.) Link. (See *E. megastachya*.)		
E. japonica (Thunb.) Trin. [Trin.]	20	(3)
E. megastachya (Koel.) Link = *E. cilianensis*	20	(3)
Eragrostis mexicana (Lag.) Link	60	(3)
E. pallescens Hitchc	80	(18)
E. spectabilis (Pursh) Steud.†	42	([6])
E. tef (Zucc.) Trotter = *E. abyssinica*	40	(3)
Erianthus arundinaceus (Retz.) Jeswiet†	40, 60	(8)
E. japonicus (Thunb.) Beauv. = *Miscanthus japonicus*	60	(7)
E. ravennae (L.) Beauv	60	(7)
Eriochloa villosa (Thunb.) Kunth	54	(3)
Euchlaena mexicana Schrad	20 b	(28)
E. perennis Hitchc	40 c	(32)
Eulalia japonica (Thunb.) Trin. = *Miscanthus japonicus*	36	(3)
Festuca amethystina L	28	(47, 48)
F. arenaria Lam.†	42	(37)
F. arundinacea Schreb. = *F. elatior* var. *arundinacea*	42 c	(44)
F. bromoides L. = F. *dertonensis*	14	(47, 48)
F. danthonii Aschers. and Graebn	28	(4)
F. danthonii Aschers. and Graebn. var. *imberbis* (Vis.) Aschers. and Graebn	42	(3)
F. dertonensis (All.) Aschers. and Graebn	14	(44)
F. duriuscula L. = *F. ovina* var. *duriuscula*	42*b	(9)
F. elatior L	14 g	(37)
F. elatior var. *arundinacea* (Schreb.) Wimm. (See *F. arundinacea*.)		
F. elatior L. subsp. *arundinacea* var. *cirtensis* St. Yves = *F. elatior* var. *arundinacea*	70	(30)
F. elatior L. subsp. *arundinacea* Hack. var. *genuina* Hack. = *F. elatior* var. *arundinacea*	42 b	(31)
F. elatior L. subsp. *arundinacea* Hack. var. *uechtritziana* (Wiesbaur) Hack. = *F. elatior* var. *arundinacea*	28	(47, 48)
F. elatior L. subsp. *pratensis* Hack. var. *apennina* Hack. = F. *elatior*	42 a	(47, 48)
F. elatior var. *pratensis* (Huds.) A. Gray = *F. elatior*	14*g	(13)
F. elatior var. *pratensis* subvar. *typica* = *F. elatior*	28	(31)
F. geniculata Cav.† [(L.) Cav.]	14	(4)
F. gigantea (L.) Vill	42 b	(30)
F. granatensis Boiss. = *F. scariosa* Lag	14 a	(30)
F. loliacea Huds	14	(43)
F. mairei St. Yves	28 a	(30)
F. maritima L	14	(4)
F. montana Savi	14 a	(30)
F. myuros L	14	(3)
F. myuros L	42 a	(47, 48)
F. ovina L	56*	(9)
F. ovina L. subsp. *alpina* (Suter) Wimm. and Grab	14 b	(31)
F. ovina L. subsp. *eu-ovina* Hack. var. *duriuscula* Hack. = *F. ovina* var. *duriuscula*	28	(47, 48)
F. ovina L. subsp. *eu-ovina* Hack. var. *duriuscula* Koch. subvar. *geniuna* Koch. = *F. ovina* var. *duriuscula*	42 b	(30)
F. ovina L. subsp. *eu-ovina* Hack. var. *duriuscula* Hack. subvar. *genuina* Hack. = *F. ovina* var. *duriuscula*	70	(47, 48)
F. ovina L. subsp. *eu-ovina* Hack. = *F. ovina*	14 b	(30)
F. ovina L. subsp. *indigesta* Hack. var. *litardieri* St. Yves = *F. ovina* var. *indigesta*	70 a	(30)
F. ovina L. subsp. *sulcata* Hack. var. *duvalii* St. Yves = *F. ovina* var. *sulcata*	42 a	(30)
F. ovina L. subsp. *sulcata* Hack. var. *panciciana* Hack. = *F. ovina* var. *sulcata*	28	(47, 48)
F. ovina var. *duriuscula* (L.) Koch. (See *F. duriuscula*.)		
F. ovina var. *tenuifolia* (Sibth.) Sm	28	(31)
F. rubra L	42 *b	(9)
F. rubra L. subsp. *eu-rubra* var. *genuina* Hack. = *F. rubra*	56	(30)
F. rubra L. subsp. *heterophylla* (Lam.) Hack. = *F. rubra* var. *heterophylla* (Lam.) Mutal	42 a	(30)
F. rubra L. subsp. *nevadensis* Hack. var. *hackelii* Lit. and Maire subvar. *brevifolia* Lit. and Maire = *F. rubra* var. *nevadensis*	70 a	(30)
F. rubra L. subsp. *violacea* (Gaud.) Hack. = *F. rubra* var. *violacea*	14	(47, 48)
F. scariosa Lag. (See *F. granatensis*.)		
F. sibirica (Griseb.) Hack. (See *Leucopoa sibirica*.)		
F. silvatica Vill	42 a	(47, 48)
F. spadicea L	14	(44)
F. spadicea var. *aurea* (Lam.) Richter. (See *F. spadicea* var. *genuina* subvar. *aurea*.)		
F. spadicea var. *genuina* subvar. *aurea* = *F. spadicea* var. *aurea*	28	(31)
F. tenuifolia Sibth.† = *F. ovina* var. *tenuifolia*	14	(37)
F. triflora Desf	14 a	(30)
F. varia Haenke. (See *F. varia* subsp. *eu-varia* var. *genuina*.)		

[6] L. M. Humphrey, personal correspondence.

Table 5.—*Chromosome numbers of various grasses*—Continued

Genus and species	Somatic chromosome number (2*n*)	Reference
F. varia var. *scoparia* subvar. *kerneri* St. Yves	28	(31)
F. varia Haenke subsp. *eskia* (Ram.) St. Yves = *F. varia* var. *eskia*	42	(47, 48)
F. varia var. *eskia* Gren. and Godr. (See *F. varia* subsp. *eskia*.)		
F. varia Haenke subsp. *eu-varia* Hack. var. *genuina* Hack. = *F. varia* Haenke	28	(47, 48)
Glyceria aquatica (L.) Wahlb.	56	(47, 48)
G. aquatica var. *arundinacea* Aschers.	28	(47, 48)
G. distans Wahl. = *Puccinellia distans*	28	(47, 48)
G. fluitans (L.) R. Br.	28	(47, 48)
G. nervata Trin. = *G. striata*	28	(47, 48)
G. plicata Fries	28	(47, 48)
G. spectabilis Mert. and Koch. = *G. aquatica*	56	(3)
G. striata (Lam.) Hitchc. (See *G. nervata*.)		
Gynerium argenteum (Nees) Stapf. = *Cortaderia selloana*	76	(19)
Haynaldia villosa (L.) Schur	14 b	(3)
Heleochloa schoenoides (L.) Host	36	(4)
Hierochloë odorata (L.) Beauv.†	42	(3)
Holcus lanatus L.	14 a	(3)
H. mollis L.	14	(47, 48)
Hordeum bulbosum L.	28	(47, 48)
H. caespitosum Scribn.	[5] 14	(50)
Hordeum caput-medusae (L.) Coss. and Dur. = *Elymus caputmedusae*	14 a	(17)
H. jubatum L.	28 c	(2)
H. jubatum L.†	[5] 14	(50)
H. murinum L.	28 b	(2)
H. murinum L.	14 a	(49)
H. nodosum L.	42	(17)
H. nodosum L†	14	(50)
H. pusillum Nutt.†	14	(50)
H. secalinum Schreb.	28 b	(47, 48)
H. silvaticum Huds.	28	(47, 48)
H. spontaneum C. Koch	14 a	(49)
Hystrix patula Moench. (See *Asprella hystrix*.)		
Imperata arundinacea Cyrillo	20	(7)
Ischaemum anthephoroides Miq.	68	(28)
Koeleria cristata (L.) Pers.	70	(4)
K. glauca (Schkuhr.) DC	14	(3)
K. panicea (Lam.) Domin	14	(4)
K. phleoides (Vill.) Pers.	26	(3)
Lagurus ovatus L.	14	(4)
Lamarckia aurea (L.) Moench	14	(3)
Leptochloa chinensis (Roth) Nees	[5] 40	(3)
L. polystachya (R. Br.) Benth.	20	(3)
Lepturus cylindricus (Willd.) Trin.	52	(19)
L. filiformis (Roth) Trin.	14	(3)
L. incurvatus Trin. = *Pholiurus incurvus*	[5] 36	(3)
L. pannonicus (Host) Kunth. = *Pholiurus pannonicus*	14	(3)
Leucopoa sibirica Griseb. = *Festuca sibirica*	28	(3)
Lolium italicum A. Br. = *L. multiflorum*	14 a	(3)
L. linicolum A. Br.° = *L. remotum*	14	(15)
L. multiflorum Lam.	14 b	(13)
L. perenne L.	14* e	(13)
L. persicum Boiss. and Hohen.	14	(15)
L. remotum Schrank. (See *L. linicolum*.)		
L. temulentum L.	14 a	(15)
Lycurus phleoides H. B. K.	40	(4)

Genus and species	Somatic chromosome number (2*n*)	Reference
Manisuris glandulosa (Trin.) Kuntze. (See *Rottboellia glandulosa*.)		
Melica altissima L.	18 b	(3)
M. ciliata L. (See *M. ciliata* Guss. var. *eligulata*.)		
M. ciliata Guss. var. *eligulata* = *Melica ciliata*(?)	18	(3)
M. micrantha Boiss. and Hohen.	18	(3)
M. nutans L.	18 a	(3)
Melinis minutiflora Beauv.	36 a	(3)
Mibora verna (Pers.) Beauv.†	14	(3)
Milium effusum L.	28	(3)
M. vernale Bieb.	28	(3)
Miscanthus japonicus (Thunb.) Anderss.	38	(8)
M. saccharifer (Anderss.) Benth.	64	(19)
M. sinensis Anderss.	42* a	(10)
Monerma cylindrica (Willd.) Coss. and Dur. = *Lepturus cylindricus*	26	(4)
Muhlenbergia glomerata (Willd.) Trin. = *Muhlenbergia racemosa*	[5] 40	(3)
M. mexicana (L.) Trin.	40	(4)
M. pungens Thurb.	42	([6])
M. racemosa (Michx.) B. S. P. (See *Muhlenbergia glomerata*.)		
M. sylvatica Torr. (See *Muhlenbergia umbrosa*.)		
M. umbrosa Scribn. = *Muhlenbergia sylvatica*	40	(4)
Nardus stricta L.	26	(3)
Nassella trichotoma (Nees) Hack. (See *Urachne trichotoma*.)		
Oplismenus burmanii (Retz.) Beauv.	72	(19)
O. compositus (L.) Beauv.	72	(4)
O. undulatifolius (Ard.) Roem. and Schult.†	54	(4)
Oryza cubensis Ekman	24	(16)
O. latifolia Desv.	48	(16)
Oryzopsis miliacea (L.) Benth. and Hook.†	24	(3)
O. virescens (Trin.) Beck	24	(3)
Panicum capillare L.	18	(3)
P. crusgalli L. = *Echinochloa crusgalli*	54	(3)
P. dichotomiflorum Michx.	54* a	(10)
P. erucaeforme J. E. Smith = *Brachiaria erucaeformis*	18	(3)
P. crusgalli var. *frumentaceum* (Roxb.) Trimen.† = *Echinochloa crusgalli* var. *frumentacea*	[5] 48	(45)
P. lindheimeri Nash	18* a	(10)
P. miliaceum L.†	42	(45)
P. miliaceum L.	36	(4)
P. miliare Lam.†	36	(45)
P. plicatum Lam. = *Setaria plicata*	54	(3)
P. sanguinale L. = *Digitaria sanguinalis*	36	(3)
P. scribnerianum Nash	18* a	(10)
P. sphaerocarpon Ell.	18*	(10)
P. subvillosum Ashe	18*	(10)
P. tsugetorum Nash	18*	(10)
Paspalum dilatatum Poir.†	40* a	(35)
P. muhlenbergii Nash = *Paspalum pubescens*	20*	(10)
P. pubescens Muhl. (See *P. muhlenbergii*.)		
P. scrobiculatum L.	40	(3)
P. stoloniferum Bosc.†	20* a	(35)
P. stoloniferum Bosc.†	20–23	(6)
P. virgatum L.	80	(4)

[5] About.

[6] L. M. Humphrey, personal correspondence.

TABLE 5.—*Chromosome numbers of various grasses*—Continued

Genus and species	Somatic chromosome number (2n)	Reference
Penicillaria spicata (L.) Willd.= *Pennisetum glaucum*	14	(4)
Pennisetum cenchroides (L.) Rich = *Pennisetum ciliare*	36	(4)
P. ciliare (L.) Link. (See *P. cenchroides*.)		
P. clandestinum Chiov.†	36 a	(29)
P. glaucum (L.) R. Br.	14*	(23)
P. longistylum Hochst.	45	(4)
P. macrourum Trin.	54	(4)
P. orientale L. Rich.	36	(3)
P. ruppelii Steud.†	27	(4)
P. setosum (Swartz) L. Rich.	54	(3)
P. typhoideum L. Rich.†=*P. glaucum*	14	(45)
P. villosum R. Br.	45	(4)
Phaenosperma globosa Munro	24	(4)
Phalaris arundinacea L.	14* d	(9)
P. arundinacea L.	28 a	(37)
P. arundinacea L. var. *picta* L.	28*	(9)
P. canariensis L.	12 b	(3)
P. canariensis L.	28	(38)
P. minor Retz	28	(3)
P. paradoxa L.	14	(4)
P. tuberosa L.	28	(7)
P. tuberosa var. *stenoptera* (Hack.) Hitchc.	28	(6)
Phleum asperum Jacq.†	28b	(3)
P. boehmeri (L.) Wibel	14 a	(3)
P. michelii All.	14*	(24)
P. paniculatum Huds. var. *annuum* (Bieb.) Griseb.	28	(3)
P. phleoides (L.) Karst.	14	(19)
P. pratense L.	42 b	(3)
Pholiurus incurvus (L.) Schinz and Thell. (See *Lepturus incurvatus*.)		
P. pannonicus (Host) Trin. (See *Lepturus pannonicus*.)		
Phragmites communis (L.) Trin.	54 a	(3)
P. communis (L.) Trin.	36 a	(51)
P. communis (L.) Trin.	48	(19)
P. communis (L.) Trin.	[5] 96	(4)
P. communis (L.) Trin.†	42*	(51)
Phyllostachys edulis (Carriere) Lehaie†	48	(52)
P. flexuosa A. and C. Riviere	54 a	(52)
P. heterocycla Mitford†	48	(52)
P. "*maliacum*" error for *P. marliacea* Mitford?	70–74	(3)
P. nigra Munro	48	(52)
P. reticulata Koch	48	(52)
Poa alpina L.	32–34	(3)
P. alpina L.	22–38	(36)
P. alpina L. var. *badensis* (Haenke) Mert. and Koch.	42	(47, 48)
P. annua L.	28 a	(3)
Do	14	(44)
P. bulbosa L.	42	(47, 48)
P. caesia J. E. Smith	42	(47, 48)
P. compressa L.	42 a	(4)
Do	56	(47, 48)
Do	14	(44)
P. glauca Vahl	70	(3)
P. nemoralis L.	28	(3)
Do	56	(36)
Do	42 a	(47, 48)
P. palustris L.	42 a	(47, 48)
Do	20	(6)
P. palustris L. var. *fertilis* (Host) Aschers. and Graebn.	28	(3)
P. palustris L.	70	(38)
P. pratensis L.	56 b	(47, 48)
Do	42	(44)
Do	28–85c	(4)
Do	49–85	(36)
Do	48–90	(1)
P. pratensis var. *angustifolia* (L.) Gaud.†=*P. pratensis* L.	28	(4)
P. pratensis var. *angustifolia* (L.) Gaud.†=*P. pratensis* L.	56	(4)
P. pratensis var. *angustifolia* (L.) Gaud.†=*P. pratensis* L.	70	(4)
P. sudetica Haenke	14	(3)
P. trivialis L.	14 a	(3)
P. violacea Bell	28	(47, 48)
Pollinia imberbis Nees	40	(3)
Polypogon littoralis (With.) J. E. Smith	42	(3)
P. monspeliensis (L.) Desf	28	(3)
Polytoca macrophylla Benth	40	(4)
Psilurus aristatus (L.) Lange	28	(3)
Puccinellia distans (L.) Parl. (See *Atropis distans* and *Glyceria distans*.)		
Rhaphis gryllus (L.) Desv. (See *Andropogon gryllus*.)		
Rottboellia glandulosa Trin.=*Manisuris glandulosa*	54	(4)
Schismus barbatus (L.) Chase. (See *S. calycinus*.)		
S. calycinus (Loefl.) Duval-Jouvet =*S. barbatus*	12	(4)
Sclerochloa dura (L.) Beauv.	14	(3)
Schleropoa rigida (L.) Griseb.	14 a	(3)
Sesleria argentea Savi	28	(4)
S. autumnalis (Scop.) F. Schultz	28	(3)
S. coerulea (L.) Ard	28*	(24)
S. tenuifolia Schrad.	42	(3)
Setaria glauca (L.) Beauv.=*S lutescens*	36	(3)
S. italica (L.) Beauv.	18 b	(3)
S. lutescens (Weigel) F. T. Hubb. (See *Setaria glauca*.)		
S. plicata (Lam.) T. Cooke. (See *Panicum plicatum*.)		
S. verticillata (L.) Beauv	36	(3)
S. viridis (L.) Beauv	18	(3)
Sinobambusa tootsik Makino	48	(52)
Sorghastrum nutans (L.) Nash.	40*	(10)
Sorghum drummondii (Nees) Hack.=*Sorghum vulgare* var. *drummondii*	20	(33)
S. effusus (Hack.) Karper and Chisholm	20	(23)
S. halepense (L.) Pers.	40	(24)
S. halepensis var. *miliformis* (Schult.) Karper and Chisholm.	40	(24)
S. hewisoni (Piper) Longley	20	(24)
S. purpureo-sericeum (Hochst.) Schweinf and Aschers. (See *Andropogon purpureo-sericeus*.)		
S. vulgare var. *drummondii* (Nees) Hitchc. (See *S. drummondii*.)		
S. vulgare var. *sudanense* (Piper) Hitchc.	20	(24)
S. versicolor Anderss	10 a	(33)
S. verticilliflorum (Steud.) Stapf	20	(23)
S. virgatum (Hack.) Stapf	20	(24)
S. vulgare Pers. (See *Andropogon sorghum*.)		
Spartina alterniflora Lois	70	(21)
S. cynosuroides (L.) Roth	80–90	(3)

[5] About.
[6] L. M. Humphrey, personal correspondence.
[7] B. L. Sethi, personal correspondence.

TABLE 5.—*Chromosome numbers of various grasses*—Continued

Genus and species	Somatic chromosome number (2n)	Reference
S. michauxiana Hitchc.=*S. pectinata*	28*	(9)
S. pectinata Link. (See *S. michauxiana*.)		
S. schreberi F. Gmel.	[5] 40	(3)
S. stricta (Ait.) Roth	56	(21)
S. townsendii H. and J. Groves	126	(21)
Sphenopus divaricatus (Gouan) Reichb	12	(3)
Sporobolus berteroanus (Trin.) Hitchc. and Chase†=*S. poiretii*	36	(4)
S. diandrus (Retz.) Beauv	36	(3)
S. indicus (L.) R. Br	18, 36	(3)
S. poiretii (Roem. and Schult.) Hitchc. (See *S. berteroanus*)		
S. tenuissimus (Mart) Kuntze	40	(19)
Stipa capillata L	44	(3)
S. lessingiana Trin. and Rupr	44	(4)
S. papposa Nees	42–44	(3)
S. pulcherrima C. Koch	44	(4)
S. sibirica (L.) Lam	24	(3)
S. stenophylla Czern	44	(4)
S. ucrainica P. Smirn	44	(4)
Themeda arguens (L.) Hack	20	(3)
T. forskalii Hack	60	(4)
Trachynia distachya (L.) Link = *Brachypodium distachyum*	30	(4)
Tragus racemosus (L.) All.†	40	(3)
Trichloris mendocina (Phil.) Kurtz	40	(4)
Tricholaena rosea Nees	36	(8)
Triodia flava (L.) Smyth. (See *T. flava*.)		
T. cuprea Jacq.=T. *flava*	42	(3)
Tripsacum dactyloides (L.) L	70	(32)
T. dactyloides (L.) L	36	(19)
T. dactyloides (L.) L.†	36, 72	(34)
T. lanceolatum Rupr	±70	(32)
T. laxum Nash	±70	(32)
T. pilosum Scribn. and Merr	±70	(32)
Trisetum flavescens (L.) Beauv	24 b	(4)
T. sibiricum Rupr	14	(4)
Uniola latifolia Michx	48	(3)
Urachne trichotoma (Nees) Trin.= *Nassella trichotoma*	38	(3)
Ventenata macra (Stev.) Boiss. and Bal	14	(3)
Vulpia alopecurus Dum.=*Festuca* sp	14	(3)
V. bromoides (L.) S. F. Gray†= *Festuca bromoides*=*F. myuros* or *F. dertonensis*	14	(47, 48)
V. myuros (L.) Gmel.†=*Festuca myuros*	42	(50)
V. myuros (L.) Gmel	14	(3)

[5] About.

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IMPROVEMENT OF TIMOTHY

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TIMOTHY is the common name applied to the species *Phleum pratense* L. About 10 species in the genus *Phleum* are known, timothy being the only one under cultivation. They are all native to northern Europe and Asia with one exception. This one, a native in North America, is *Phleum alpinum* L., alpine timothy—a grass that occurs throughout the mountainous regions in the western United States, and in the East as far south as the White Mountains of New England (*20, p. 122*).[1]

While timothy is of European origin, it was in the United States that it was first brought under cultivation. The early history of the crop in this country is somewhat obscure, but mention of it in colonial days is not uncommon. In New England it was known as herd's grass at least as early as the first part of the eighteenth century—probably earlier. The name "timothy" is said to have been derived from Timothy Hansen, who obtained seed from New England or New York and introduced it into Maryland, and possibly into some of the other southern Colonies, about 1720. Sometime after 1740 an early agriculturalist, Jared Elliott, sent seed from Connecticut, under the name of herd's grass, to Benjamin Franklin. In a letter dated July 16, 1747, Franklin wrote that the grass sent to him "is grown up and proves mere timothy"—indicating that it had become fairly well established as a hay crop in Pennsylvania at that time (*21*). From then on the crop increased in use and importance and has received more attention from agriculturists than any other grass.

In 1909, according to the United States census report, there was a total of 34,228,000 acres of timothy grown alone and in mixture with clover. In 1929 this acreage had decreased to 25,547,000, but it still constituted 37.7 percent of the total acreage used for the production of all kinds of hay in that year. In 1928, the last year in which separate estimates were made by the United States Department of Agriculture of the acreage of timothy alone and in mixture with clover, timothy was grown alone on 8,537,000 acres and with clover on 16,078,000 additional acres.

For feeding horses, of which there are still large numbers, no other hay has been found as generally satisfactory as timothy. The cost of the seed is less than that of most meadow and pasture grasses and it can be sown more readily with the implements used for sowing clover and alfalfa. Although alfalfa produces hay superior to timothy

[1] Italic numbers in parentheses refer to Literature Cited, p. 1116

in yield and in percentage of protein, timothy grows well on many soils on which alfalfa or even clover cannot be produced without a considerable investment for lime or drainage. Timothy is very extensively grown for hay in mixture with clover, and alfalfa can be more readily grown on some soils not naturally suited to it if it is sown in mixture with timothy. As a pasture grass, timothy is more palatable to livestock than many other grasses, including redtop, orchard grass, and Kentucky bluegrass; and the recent increased interest in pastures has created an interest in the possibility of developing varieties of timothy especially adapted for use in pasture mixtures.

HISTORY OF TIMOTHY IMPROVEMENT

Early Efforts to Improve Timothy

According to available information, the first efforts to develop improved strains of timothy were made in the United States. No improved varieties were in existence at the close of the last century, as there were of corn, oats, wheat, and other crops. The appreciation of the wide diversity in timothy plants, which made varietal improvement possible, and the prospect of benefits to the producers of timothy hay, both for market and for use on the farm, if varieties were available that would produce larger yields of better quality than ordinary timothy, created incentives for the breeding programs that were undertaken at this time by several experiment stations and other agricultural organizations.

Figure 1.—Willet M. Hays, the earliest breeder of timothy.

Willet M. Hays, professor of agriculture at the University of Minnesota (fig. 1), made in 1889 a number of selections of timothy plants. He had observed the wide variation in plants of ordinary timothy and thought that by selecting the best from among them it would be possible to develop varieties, suited for growing in mixture with clover, that would prolong the season when timothy could be harvested in condition to make a high grade of hay, and also varieties capable of producing larger yields (*13*). No records have been found of any earlier attempt to improve timothy in this way, although Sinclair recorded the development of varieties of perennial ryegrass, through selection, more than a century ago (*23, pp. 212–213*). Hays discontinued his own work with timothy, but afterward, as the first secretary of the American Breeders' Association and as Assistant

Secretary of the United States Department of Agriculture, he took an active interest in the improvement of this crop.

In 1894, a few years after Hays made his first selections, A. D. Hopkins (fig. 2), then entomologist at the West Virginia Agricultural Experiment Station, selected a number of timothy plants at his farm at Kanawha Station, W. Va. (*14, 15, 16*). He continued this work for several years, making new selections and conducting tests of them, for the purpose of eventually producing varieties with better quality and higher yielding capacity than the single unimproved strain then available. In 1899 he distributed plants of some of his selections to the Department of Agriculture and to a number of State agricultural experiment stations. In 1902 he became forest entomologist and chief of the Division of Forest Insects, Bureau of Entomology, Department of Agriculture, but continued his work with timothy on his farms in West Virginia. About 1907 or 1908 he transferred additional selections he had made to the Division of Forage Crops of the Department.

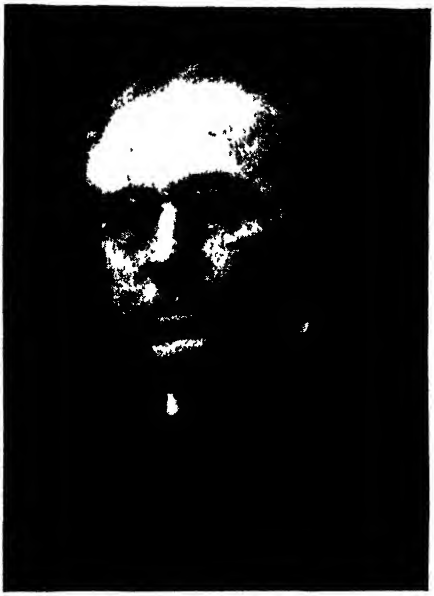

Figure 2.—**A. D. Hopkins, who developed the first varieties of timothy of which plants and seed were distributed.**

Hopkins increased the stock of seed of three of his selections and introduced them as new varieties. Seed was distributed by him and by the Department to a number of farmers and experiment stations. One of these varieties, Hopkins Early, headed and bloomed at somewhat more nearly the same time as medium red clover than ordinary timothy and thus was better for growing in mixture with this clover. Stewart Mammoth, derived from a vigorous, long-stemmed plant, was slightly later and was thought capable of producing somewhat larger yields than ordinary timothy. The third variety, Pasture timothy, did not differ greatly in habit of stem growth from the ordinary strain used for hay, but its leaves tended to remain green late, and, as its name suggests, it was thought well suited for pastures.

Timothy Improvement by State Experiment Stations

One of the cooperators to whom A. D. Hopkins distributed plants or seed was T. F. Hunt, of the Ohio State University. When Hunt went to the College of Agriculture at Cornell University, Ithaca, N. Y., in 1903, he immediately began a timothy-breeding program. His objective was the development of varieties that would give a larger yield of superior-quality hay, and he also wished to study some of the fundamental principles upon which a timothy-breeding program should

be based. Seed was obtained from a large number of sources in the United States and from foreign countries. Plants were grown in row test plots, and from them many variants were obtained as the basis for further selections. When Hunt went from Cornell University to the University of California, the timothy-breeding investigations were continued by H. J. Webber and his associates. At the present time, the timothy-breeding work at Cornell is under the direction of C. H. Myers. A number of technical studies of timothy, the variations occurring in it, and methods of improving it have been described in different published articles. Two varieties have been developed at Cornell, and efforts are now being made to have seed of them introduced commercially. One is somewhat earlier than ordinary timothy; the other is later and produces relatively large yields; both tend to be rust-resistant.

During the period from 1911 to 1924 the Iowa Agricultural Experiment Station tested about 300 timothy selections. Seed of the most outstanding one of these was increased and distributed to Iowa farmers, but the strain was finally lost. In Minnesota the early work started by Hays in 1889 was later discontinued, but in 1916 work was again resumed by others. Early work in timothy improvement was also conducted at the Pennsylvania station, starting in 1908, but was discontinued in 1931. Other stations that have more recently carried on work in timothy improvement are those of Kentucky, New Jersey, and Wisconsin.

Timothy Improvement
by the United States Department of Agriculture

The earliest timothy-breeding work conducted by the United States Department of Agriculture was undertaken in 1899 by F. Lamson-Scribner, Chief, and Thomas A. Williams, Assistant Chief, of the old Division of Agrostology, with tests of some of the selections received from A. D. Hopkins, then at the West Virginia Agricultural Experiment Station. When the Office of Forage Crops—now the Division of Forage Crops and Diseases—of the Bureau of Plant Industry was organized in 1903, C. V. Piper, who was in charge, became interested in timothy improvement. From that time until 1909 a number of new selections of leafy, vigorous timothy plants were made. Tests were conducted at the Arlington Experiment Farm, Arlington, Va., of the new selections in comparison with some of Hopkins' selections, and also in comparison with selections obtained from the New York (Cornell) Experiment Station. The timothy-improvement program, however, did not receive a very great amount of attention until a decade later when the Timothy Breeding Station was established in cooperation with the Ohio Agricultural Experiment Station. This work was conducted first at New London, Ohio. It continued from 1909 to 1915, when the station was reestablished on a larger area of land at North Ridgeville, Ohio. Here the work was conducted until 1935, when it was transferred to the Ohio Agricultural Experiment Station at Wooster. The outstanding varieties developed in this work are Huron and Marietta, described later under the heading Improved Varieties.

Timothy Improvement in Foreign Countries

. Since the breeding of timothy was first undertaken in the United States, similar work has been conducted in Canada and in several countries in Europe.

Some of the earliest European work was done at the Plant Breeding Institute at Svalöf, Sweden. Several varieties have been developed there, some of which are adapted to different regions, as southern Sweden, middle Sweden, and northern Sweden, where winter hardiness is an essential characteristic.

Timothy-breeding investigations were undertaken at the Welsh Plant Breeding Institute at Aberystwyth, Wales, somewhat later than at Svalöf, and have been conducted on an extensive scale. Varieties suitable for hay production in Great Britain have been developed from native timothy plants. Other varieties, characterized by relatively small low-growing plants with procumbent stems that tend to become rooted at the nodes, have been found of value in pastures in Great Britain especially when grown in mixture with white clover. A third type of timothy, midway between the typical hay-producing type and the extreme pasture type, classified as "hay-pasture" timothy, also has been developed. The methods used in timothy breeding at Aberystwyth have been described by Jenkins (*17*).

Timothy-breeding investigations are also being conducted at agricultural experiment stations in Scotland, Belgium, Denmark, Germany, the Union of Soviet Socialist Republics, and possibly elsewhere.

OBJECTIVES IN TIMOTHY BREEDING

It is comparatively easy to develop, within a few generations, a strain of timothy in which some single character, such as earliness or lateness, long stems, freedom from rust, or tendency to produce large yields, is reproduced fairly well in the plants grown from seed. To produce a variety in which all of the desirable characteristics are combined is a much more difficult task. Furthermore, a certain variety of timothy may be adapted only to a more or less restricted area. For instance, in northern Sweden the Bottnia variety is valuable because it is very winter-hardy, but in northern Ohio it apparently has no practical value because it produces smaller yields of hay than other varieties that are sufficiently hardy in this latitude. Some of the late varieties that have produced relatively large yields of high-quality hay in northern Ohio are of no value in Kentucky or farther south. It is therefore necessary to have varieties for certain regions as well as for different uses, and this must be recognized in any well-formulated breeding program.

The most common disease of timothy is rust. Although plants in meadows are not often entirely destroyed by it, yet the growth of those that are badly attacked is checked, and the leaves dry up prematurely. Some plants are more susceptible than others. Selection for rust-resistant strains has been one of the objectives of most breeders of timothy. When plants relatively free from rust have been selected, it has been found that their progeny tend to be rust-resistant. In an investigation conducted at MacDonald College, Quebec, Canada, Bird (*2*) found that, generally speaking, the majority of improved

strains of timothy tested showed marked resistance to rust. Although strains differed greatly in their reaction to the disease, the reaction of individual plants within strains also varied greatly. No strains were found entirely free from the disease. Strains from Scandinavia were generally highly susceptible to rust, yet Gloria and Øtofte, two improved varieties, were outstanding in their resistance.

Some of the earliest public discussions of the possibility of producing improved varieties of timothy, as of other farm crops, took place at the meetings of the Society for the Promotion of Agricultural Science, attended by many of the leading agricultural scientists of the last decade of the past century and of the first decade of the present one. A great deal of interest was aroused by Hopkins' papers on the improvement of timothy. He described many variations, such as early plants in condition to cut for hay about the same time as red clover and late plants producing hay that would retain green leaves and high quality for a longer time than ordinary timothy, and showed the possibilities for developing distinct varieties. Here, it seemed, was a new field of opportunity for service to agriculture. At the meeting at Columbus, Ohio, in 1899, Hopkins said that because of the pressure of official duties he thought he would have to give up his work with timothy. W. J. Beal, of the Michigan Agricultural College, one of the leading American botanists of that time, and also others protested that Hopkins should rather give up his work with insects in order that he might be able to devote all of his time to the improvement of timothy.

Present Search for Leafy Pasture Varieties

The present interest in improved pasture grasses has developed within the last 10 years.

As already noted, pasture varieties of timothy already have been developed and introduced in farm practice by some of the European agricultural experiment stations or plant-breeding institutes. When sown in fields to be used as permanent pastures, these varieties continue to form a better and more persistent turf than ordinary timothy.

At the New York Agricultural Experiment Station (Cornell), excellent results have been obtained with Aberystwyth Pasture timothy S. 50 when grown in association with wild white clover under conditions of close grazing.

In general, these low-growing European types of timothy produce very little seed in the latitude of Ohio; for normal development they require the longer days in spring and summer that occur farther north. If they are used, it may be necessary to have the seed produced relatively far north, either in North America or in Europe, and to import it into localities where it is to be sown in pastures.

Long before any of the special pasture varieties of timothy were introduced, ordinary unimproved American timothy had been used for pasturage. Farmers in the United States very commonly turn their farm stock into meadows during late summer or fall, after the first hay crop has been removed. It is also a common practice to utilize timothy meadows from which hay crops have been harvested as all-season pastures for 1 or more years before plowing for some other crop.

It is not unlikely that some of the improved varieties of timothy, selected primarily for their usefulness in meadows, may also be superior to ordinary timothy for use in pastures.

Variations a Basis for Improvement

Ordinary American timothy plants vary within quite wide limits in season of maturity, length and degree of fineness of stems, breadth of leaves, degree of susceptibility to rust, tendency for the leaves to remain green as the seeds approach maturity, and in other ways. These numerous variations and the different ways in which they are

Figure 3.—A timothy plant of the pasture type grown from seed from northern Europe.

combined in different plants result in a very wide range of variants from which selections may be made.

In Europe, as in the United States, wide variation in timothy plants is common and some of these variants offer special opportunity to the breeder. A form occurs in extreme northern Europe that is entirely distinct from any found in the United States. Plants of this form grown in the latitude of northern Ohio are characterized by short stems, which usually grow more or less procumbent upon the surface of the soil (fig. 3) instead of upright like the stems of ordinary American timothy (fig. 4). Relatively few of the stems have heads, the florets bloom late, and the seed frequently does not form or fails to mature. Some of the more extreme plants of this northern European form produce no heads when they are grown as far south as northern Ohio.

Methods of Developing New Varieties

Timothy is generally cross-pollinated. Experiments have demonstrated, however, that when pollen from the same plant is used to fertilize the florets, usually a small percentage of them produce seed.

Cross-pollination results in the occurrence of many natural hybrids between plants of diverse types. This provides a wealth of forms from which selections may be made, but makes the maintaining of a new variety more difficult.

The method used in the timothy-improvement work conducted by the Department in cooperation with the Ohio Agricultural Experiment Station is as follows:

Seed from single-plant selections is sown in a seedbed or in a small broadcast plot. The growth of the plant of different selections is observed and compared in these plots, and plants are taken from them and transplanted to cultivated row plots where each individual plant has ample space for development. Later, from the row plot of each strain, one or more new selections are made of the plants most outstanding for the desired qualities. When, as a result of repeated observations and tests, a selection of sufficient merit is finally developed, the supply of seed is increased, and it is introduced under an appropriate name as a new variety.

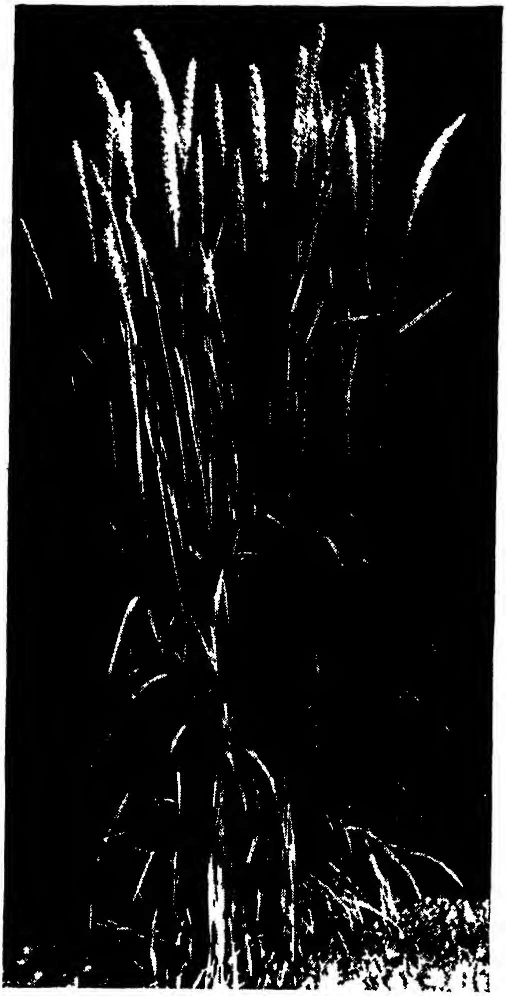

Figure 4.—A timothy plant having the relatively long, upright stems characteristic of the American forms.

Since no provision is made during the early stages of selection to prevent the florets of the plant or plants of one selection from becoming fertilized with the pollen produced by plants of other strains, the method is known as that of selection with open pollination. Experiments conducted over a number of years have shown, however, that when selection for some particular quality or character is continued through several generations plants may be developed that reproduce themselves through seed fairly true for this character (*6*).

At some other experiment stations or plant-breeding institutions the seed of selected plants has been produced from self-fertilized florets, that is, florets fertilized with pollen from the same plant. In this way it is possible to develop selections or varieties in which the plants conform to a certain type more closely than if they grew from seed produced under open pollination. In some strains of timothy

this uniformity is attained only at the cost of much loss in vigor. Our general knowledge of the science of plant breeding indicates that this deterioration may be overcome later by artificially cross-pollinating two established uniform strains and producing a hybrid in which some of the most desirable characteristics of both parents are combined.

At other places where timothy breeding is being conducted both open-pollination and self-pollination are used, one method sometimes alternating with the other from generation to generation.

When a variety of timothy is finally established and its seed is being increased and produced on a larger scale, it is essential that indiscriminate cross-pollination with ordinary timothy or other varieties be avoided, or else the peculiar characteristics by which the variety is distinguished are likely to disappear.

Improved Varieties

Though no improved timothy varieties were available at the close of the past century, at the present time there are a number that are as distinct from one another as varieties of corn, oats, or wheat.

Among those available commercially in the United States are Shelby, Huron, and the recently developed Welsh pasture strain, of which very limited quantities of seed have been imported from Great Britain within the last 2 or 3 years.

In other countries, additional varieties, mentioned in table 1 in the appendix, have been introduced.

The Shelby, an early-maturing variety grown in southern Indiana for many years, apparently is the result of regional selection. William Zoebel, of Shelbyville, Ind., producer of the variety, grew his own timothy seed from about 1855 until the time of his death in 1892, and his two sons continued the practice. Most of the Shelby timothy grown on other farms in the vicinity can be traced to the Zoebel farm. The relative time of maturity of this timothy when William Zoebel began growing it is not known. The information available, however, indicates that the characteristic of earliness developed gradually by natural selection. Zoebel harvested his timothy for hay when the earliest heads were mature. Some of the seeds from the ripe heads shattered in the mow, or where the hay was thrown down to the floor below. The mixed chaff and seed was swept up and the seed was separated with the fanning mill. This process, which was repeated year after year and continued at least up to 1930, supplies an explanation of the origin of the variety that is satisfactory and may be assumed to be correct. Little or none of the seed is shipped away from the vicinity. Many farmers of the district who do not produce their own seed purchase seed of Shelby timothy if it is available. If it is not they get seed of ordinary timothy from somewhere else. Thus the early variety and ordinary timothy have been grown on different farms in the same locality, but Shelby timothy has retained the characteristic of earliness.

The Huron is a late-maturing variety developed in Ohio. Plants grown from the seed of Huron timothy are shown in figure 5 (*5*).

In 1911 the plant from which this variety originated was found growing along a road near Wakeman, in north-central Ohio. It was transplanted to the timothy breeding station at North Ridgeville where it was grown in experimental tests. Seed was later distributed to agricultural experiment stations in other States. In the Pacific Northwest, in nearly all trials, the yields have been larger, the plants have remained in condition to make a good quality of hay later in the

Figure 5.—The six plants at the right, grown from seed produced by the original plant of Huron timothy, are more uniform and are more vigorous and larger than the six plants of ordinary timothy at the left.

season, and they have continued to grow for a longer time in pasture mixtures than ordinary timothy. The Huron is now most extensively grown in northeastern California and western Oregon, though it has been found well-adapted to unirrigated land in northwestern California and western Washington, as well as to the irrigated and moister valleys of eastern Oregon, eastern Washington, and northern Idaho. The use of the variety, especially in pastures in mixture with other grasses and clovers, has been gradually expanding. It was estimated at the Oregon Agricultural Experiment Station early in 1936 that, in addition to its being used on several hundred acres seeded to this variety alone, it has probably been sown in pasture mixtures on at least 8,000 to 10,000 acres.

Another selection developed at the timothy breeding station, North Ridgeville, Ohio, is about to be introduced under the varietal name Marietta. In northern Ohio it is 4 or 5 days earlier and in southern Ohio about a week earlier than ordinary timothy. Tests have demonstrated that it yields more than ordinary timothy, especially in the latitude of southern Ohio. It arrives at a stage of development suitable for cutting for hay at more nearly the same time as medium red clover or alfalfa than does ordinary timothy. The Ohio Seed Improvement Association is planning to assist in the introduction of Marietta timothy into farm practice in those parts of the State to which it is well adapted.

Since the primary objective in most timothy-breeding programs is increased hay production, most of the improved varieties developed

to date are primarily hay varieties. Some of them, like that shown in figure 6, *A*, are earlier than ordinary timothy. One of the characteristics of an early timothy is that it is capable of producing elongated stems with heads, and the florets bloom and seeds form on them under shorter days than are required for late varieties, such as the one in figure 6, *B*. For this reason, early varieties can produce a hay crop in the South, where the days during spring and summer

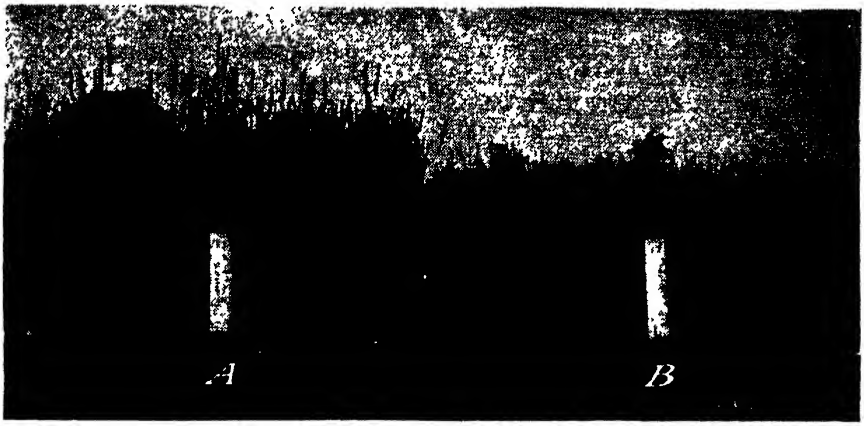

Figure 6.—*A*, A plot of early timothy, full-headed and beginning to bloom; *B*, a plot of late timothy, with stems grown to only a part of their full length. Photographed at North Ridgeville, Ohio, June 20, 1933.

are too short for the proper development of late varieties. Trials in southern Ohio and at the Kentucky Agricultural Experiment Station have demonstrated the correctness of the theory that near the southern border of the timothy-producing area in the United States early varieties produce materially larger yields of hay than late varieties.

Distribution of Improved Varieties

In Sweden certain organizations formed for the purpose of introducing the seed of new and improved varieties of all kinds of farm crops have been instrumental in having some of the new varieties of timothy grown. No organized effort of this kind has yet been made on a large scale in the United States.

At Cornell University and in Ohio seed has been distributed to farmers who expect to harvest a seed crop. The same method is used in Ontario, Canada. In Quebec the seed is sent to the Provincial seed farm and from there to Provincial seed centers. In Great Britain improved strains are now being grown on a commercial scale by seedsmen. In Sweden all seed is sold and distributed by the Svalöf Seed Co., which has a monopoly on all varieties produced by the Swedish Seed Association.

The increased cost of seed must always be taken into consideration in the establishment of new crop varieties. The seed of improved varieties of timothy necessarily sells at a somewhat higher price than that of ordinary unimproved timothy. This is because the seed

grower must use extra care not to have any ordinary timothy plants growing in mixture where seed of the improved variety is being produced. Further, if the seed is certified, the cost of inspecting the meadow must be added. However, the total quantity of timothy seed required for establishing 1 acre of meadow is so small that the slight additional cost for the improved seed should be no objection if the varieties are distinctly superior.

Since relatively long days are required for their development (*7*), it appears probable that the usefulness of late varieties of timothy will be restricted to latitudes no farther south than the northern part of Ohio (*8*). When grown under suitable conditions, it has been found that the better late varieties produce somewhat more hay than ordinary timothy, though usually these increases in yield per acre do not exceed a few hundred pounds. The leaves on the best late selections remain green for a longer time than those of ordinary timothy, and consequently the protein content and quality of the hay remain at a relatively high level for a longer time. On farms in the northern part of the United States, where relatively large acreages of clear timothy hay are harvested and where there is difficulty, because of unfavorable weather conditions or the pressure of other farm work, in harvesting ordinary timothy early enough to produce hay of a high quality, late varieties would have certain advantages.

Timothy is now being grown in mixture with alfalfa in an increasing area each year (*1*). This mixture should be harvested early, before ordinary timothy has begun to bloom. It is apparent, therefore, that an early variety of timothy, that would be in bloom when the crop should be harvested, is most suitable for such a mixture and should be supplied by the timothy breeder.

No varieties of timothy that are primarily pasture types have yet been produced in the United States. The Welsh pasture variety, seed of which is now available to a limited extent, is characterized by its short, low-growing stems, and it would produce much smaller yields of hay than any of the hay types. There has been so little experience in this country with the European pasture varieties, even experimentally, that it is not yet clear just how useful they may be.

As indicated in the preceding paragraphs, the principal objectives in the improvement of timothy are the development of rust-resistant varieties; early varieties suited to the southern part of the timothy-growing area; late varieties for the North, for use where timothy meadows are maintained for 2 or more years; varieties adapted for hay production when grown in mixture with clover or alfalfa, and varieties for use in pastures

TECHNICAL RESEARCH [2]

When T. F. Hunt began the timothy-breeding investigations at Cornell University in 1903, seed was procured not only from many different places in the United States and Europe but also from other countries. The plants grown from these lots of seed revealed the

[2] This section is written primarily for students and others professionally interested in breeding or genetics.

existence of a very wide range of types (*26*). Some of the strains at Cornell were used by Clark (*3*) in a technical study of variation and correlation in timothy. Smith and Myers (*24*) have recently published the results of a biometrical analysis of yield trials.

Investigations at MacDonald College on the rust resistance of improved strains have been previously referred to.

Gregor and Sansome (*10*) found that the low-growing forms of timothy plants with more or less procumbent stems, which occur in Great Britain, have 14 chromosomes ($2n$), whereas the plants with longer, more nearly upright stems have 42 chromosomes ($6n$). Plants of the latter type, which occur both in Europe and in North America, were designated by these authors as the "American" and the low-growing forms as "British Wild" type. Gregor at first found these two types are intersterile (*9*), but according to a recent report (*18*) they later were able to produce artificial F_1 hybrids between them.

Sethi, in a study conducted in India of *Phleum*, *Phalaris*, and *Festuca*, found seven as the basic chromosome number in each genus (*22*). In *Phleum*, while different morphological types interbreed quite readily provided they have the same number of chromosomes, diploid and hexaploid types can be crossed only with great difficulty.

At the Plant Breeding Station at Svalöf, Sweden, Muentzing (*19*) observed and studied spontaneous hybrids between *Phleum pratense* and *P. alpinum* ($4n$). Some of these hybrids were approximately pentaploid.

The extent to which timothy florets produce seeds under conditions of self-pollination has been studied by Witte (*27*), Valle (*25*), and other European investigators. In general, it has been found that when they are self-pollinated the average percentage of florets producing seeds is very much less than under natural conditions that permit cross-pollination.

A series of genetic studies of timothy has been conducted at the Minnesota Agricultural Experiment Station. Hayes and Barker (*11*) found that there is a considerable amount of variation in the extent to which timothy may be self-pollinated. Some plants are highly self-sterile, others are highly self-fertile. Clarke found that although a few of the selfed lines were markedly reduced in vigor the majority compared favorably in yielding ability with the open-pollinated commercial strains (*4*). He observed that when timothy seeds are produced by self-fertilized florets for a few consecutive generations the plants grown from these seeds are more uniform than plants grown from seed from open-pollinated florets.

Hayes and Clarke, in an investigation conducted at the Minnesota Experiment Station (*12*), found that selection in self-fertilized lines is a logical means of freeing the lines of undesirable recessive characters and of obtaining vigorous lines that excel in such important characters as yielding ability and disease resistance. On the other hand, it has also been found elsewhere (*6*) that when selection for any particular type is continued, even under natural conditions favorable for open pollination, the plants of many strains representing several generations of selection show a high degree of uniformity.

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APPENDIX

Table 1.—*Introduced varieties of timothy*

Location and institution	Breeder	Variety and year introduced	Characteristics	Breeding methods	Parental material	Estimated acreage, 1936
United States:						
Cornell University, New York Agricultural Experiment Station.	C. H. Myers, W. I. Fisher.	Cornell 1777, 1922	Good yields; rust-resistant; medium early.	Selection of outstanding plant followed by selfing.	Commercial stocks	Limited.
	do	Cornell 4059, 1922	Good yields; late	do	do	Do.
Ohio Agricultural Experiment Station cooperating with U. S. Department of Agriculture.	Morgan W. Evans	Huron, 1933	Late, leafy, rust-resistant.	Selection	Plant growing along roadside in northern Ohio.	About 8,000 to 10,000 acres for hay and pasture.
	do	Marietta, 1936	Medium early, leaves remain green well, rust-resistant.	Selected through 3 generations with open pollination.	Plant growing in an old meadow in northern Ohio.	About 50 acres.
Canada:						
Central Experimental Farm, Ottawa.	O. Malte, R. I. Hamilton, G. P. McRostie	Boon, 1923	Heavy-yielding hay type; rust-resistant	Controlled mass selection and suitable tests to evaluate strains.	Wild plants from Alberta, Canada.	About 300 acres for hay and seed.
College of Agriculture, Alberta.	F. R. Fryer	Swallow, 1926	Leafy hay type	Maternal line selection with open-pollination in isolated plots	Svalöf 523 from Sweden	Quite extensive in northern Alberta.
Ontario Agricultural College, Guelph.	O. M. McConkey	O. A. C. No. 1, hay type, 1934.	Leafy, rust-resistant	Inbreeding and selection	Danish material	1 acre.
	do	O. A. C. No. 1, intermediate type, 1933	Leafy, late	do	Swedish genotypes	Increase block.
	do	O. A. C. No. 1, pasture type, 1933.	Persistent bottom grass	do	Russian genotypes	Do.
MacDonald College, Quebec.	J. Norman Bird.	Montcalm, 1932	Rust-resistant, superior yields	Combination of selfed lines.	Svalöf Nos. 237-A and 523, Sweden.	
	do	Milton, 1936	Rust-resistant, good yields, early.	Selected plants allowed to outcross with other selected plants of same type.	Minnesota Nos. 79 and 81, Svalöf 523, Cornell 1676, F. C. 12468 (Ohio).	10 acres.
Great Britain:						
Aberystwyth, Wales	T. J. Jenkins	S. 48	Persists under grazing; leafy; rust-resistant; hexaploid.	Selection and hybridization intermingled.	Selected British indigenous plants.	About 47 acres for seed production.
	do	S. 50	Exceptionally persistent under grazing, creeping; diploid.	do	From very old British pasture.	About 18 acres for seed production.
	do	S. 51	Very leafy hay type; winter-green; rust-resistant; hexaploid	do	Selected British plants	About 61 acres for seed production.

Craig's House, Corstorphine, Edinburgh, Scotland.	J. W. Gregor	C b 191	Diploid; stems ascending about 2 feet; persistent bottom grass for pastures.	Selection and hybridization.	Wild plants from east Scotland.	4¼ acres for seed production.
Sweden:						
Svalöf	H. Witte	Gloria, 1920	High yield; rust-resistant.	Selection	Swedish wild plants	Large.
	S. O. Berg	Weiball Kampe II, 1933.	do	do	do	Do.
	George Nilsson	Bore, 1929	Winter hardy	do	do	Considerable.
Lulea	A. Uhlander	Bottnia, 1929	do	do	do	Do.
Landskrova	B. Kajanus	Weiball Kampe I, 1922.	High yield, rust-resistant.	do		Large.
Norrkoping	Algot Holmberg & Son.	Svea				

TABLE 2.—*Timothy-breeding projects*

Location and institution	Date	Personnel: Present	Personnel: Past	Nature of work to date	Suggested work for future
United States:					
Agricultural Experiment Station, Ames, Iowa.	1911–24	None		Selection	Development of pasture types.
Agricultural Experiment Station, Lexington, Ky.	1935–	E. N. Fergus		Mass selection	Photoperiodism in relation to varieties.
Agricultural Experiment Station, St. Paul, Minn.	1889–92 1916–	H. K. Hayes, I. J. Johnson, C. W. Doxtator, H. K. Schultz, W. M. Myers.	W. M. Hays, H. D. Barker, Sidney Clarke, F. R. Immer.	Selection, hybridizing, cytology, comparative testing.	Determining the nature of self-fertility; effects of inbreeding; effects of crossing.
Agricultural Experiment Station, New Brunswick, N. J.	1924–	H. B. Sprague, R. E. Blaser, M. E. Paddick.	E. E. Evaul, N. F. Farris, W. G. Colby, N. C. Curtis.	Selection	Development of leafy type for pasture; inheritance studies; extent of natural cross-fertilization.
New York (Cornell) Agricultural Experiment Station, Ithaca.	1903–	C. H. Myers, W. I. Fisher	T. F. Hunt, J. W. Gilmore, Samuel Fraser, H. J. Webber, C. F. Clark, H. F. Smith.	Line selection	Development of pasture types; cause of sterility.
Ohio: Agricultural Experiment Station and U. S. Department of Agriculture cooperating:					
New London	1909–15	M. W. Evans	C. V. Piper, R. A. Oakley	Selection	Studies of relation of length of day and of latitude to the growth of early, medium, and late timothy and the effects of outcrossing with improved strains of similar types.
North Ridgeville	1915–35	do	do	do	Do.
Wooster	1935	do		do	Do.
Agricultural Experiment Station, State College, Pa.	1908–31	None	C. F. Noll	Selection, inbreeding	Development of early strains for growing with clover, and late strains to prolong the harvesting season.
Arlington Experiment Farm, U. S. Department of Agriculture, Arlington, Va.	1899–1908	do	F. Lamson-Scribner, T. A. Williams, C. V. Piper.	Selections	
Agricultural Experiment Station, Kanawha Station and Morgantown, W. Va.	1894–1908	do	A. D. Hopkins	do	
Agricultural Experiment Station, Madison, Wis.	1936–	O. S. Aamodt, F. Tinney, A. H. Ahlgren.		Selection, cytology, development, of hay and pasture varieties.	Fertility study of different strains.

Canada:					
Central Experimental Farm, Ottawa.	1912–	R. McVicar	O. Malte, R. I. Hamilton, G. P. McRostie.	Mass selection for hay and pasture varieties.	Development of pasture-hay types with disease and cold-resistance and high seed-yielding capacity.
College of Agriculture, Edmonton.	1918–	J. R. Fryer		Selection and selfing	Study of reduced fertility from selfing; effects of crossing; genetic studies.
College of Agriculture, Guelph	1923–	O. McConkey		Genetics, cytology, mass selection, and inbreeding.	Development of leafy rust-resistant varieties compatible in mixtures; collection of breeding material from northern latitudes.
MacDonald College, Quebec	1914–	J. N. Bird	L. S. Klinck, L. A. Waitzinger, G. P. McRostie, A. McTaggart.	Selection with open-pollination with selected plants of a similar type.	The development of strains producing more aftermath.
Wales:					
Plant Breeding Station, Aberystwyth.	1920–	T. J. Jenkins		Selection and hybridization; technique and rust-resistance; cytology.	Genetics of various types, to determine minimum number of interrelated plants that can be used in strain building without loss of vigor.
Scotland:					
Craig's House, Corstorphine, Edinburgh.	1923–	J. W. Gregor		Selection and hybridization	Physiology of breeding material, and development of trial technique for evaluation of characters other than yield.
Belgium:					
Plant Breeding Station, Ghent.	1935–	R. Govaert		Selection	
Sweden:					
Swedish Seed Association, Svalöf.	1904–	G. Nilsson-Leissner, N. Sylven, A. Müntzing, F. Nilsson, G. Nilsson, J. E. Siden, F. Naesman.	H. Witte, A. Uhlander	Selection, inbreeding, and subsequent crossing; inheritance.	Development of winter-hardy, high-yielding types resistant to lodging; creeping types for pasture; types with high nitrogen content and superior ability to utilize nitrogenous manure.
Weibullsholm Plant Breeding Station, Landskrona.		A. Akerberg	B. Kajanus, O. Berg		
Otto J. Olson & Son (seedsmen), Hammenhög		E. Nilsson			

ALFALFA IMPROVEMENT

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ALFALFA means "best fodder" in Arabic, the language from which the crop received its name. Botanically it is known as *Medicago sativa* L. In England and most other European countries it is called lucerne, perhaps after Lake Lucerne and Lucerne Canton, in Switzerland, where alfalfa was grown at an early date, though some believe the name was derived from the Spanish or the French.

Alfalfa is a member of that large and important group of plants called the legume or pea family, characterized by ability to provide a home for useful bacteria that take nitrogen from the air and store it in a form available to plants, thereby enriching the soil. The home for nitrifying bacteria is on the roots in what are known as nodules, which look like small detachable lumps or knots. The soil-improving value of legumes, combined with their forage values, makes them one of the great economic plant families.

In 1929 alfalfa hay was produced on approximately 35 million acres throughout the world, according to Klinkowski (*19*).[2] In addition, a proportionately large acreage was devoted to alfalfa-seed production in those regions where climatic and soil conditions are conducive to seed

[1] The authors gratefully acknowledge the assistance of N. I. Petersen, who prepared the key on the common species of *Medicago*.

[2] Italic numbers in parentheses refer to Literature Cited, p. 1147.

THE ***most serious threat to alfalfa growing in the United States is the insidious disease, bacterial wilt, which kills stands of susceptible alfalfa in 2 to 4 years. In the large area where this disease is present—and it is spreading to other areas—it annually destroys hundreds of thousands of acres of alfalfa, with aggregate losses equivalent to those that would be experienced by farmers as a result of flood, drought, or any other major disaster. If varieties or strains could be developed that were sufficiently resistant to maintain stands even 2 years longer, these farmers would be saved many millions of dollars. This is one of the problems on which alfalfa breeders are now working, and promising progress has been made.***

setting and maturity. Argentina reported 14 million acres of alfalfa hay in 1929, the United States nearly 12 million acres (fig. 1), and France 3 million acres. Other countries reported smaller acreages, but the crop was widely distributed. Since 1929 the aggregate acreage of alfalfa is believed to have extended, but there are no available figures to support this belief.

There are many types of alfalfa, and they display wide differences in their adaptation to environmental changes from the Mexican to the

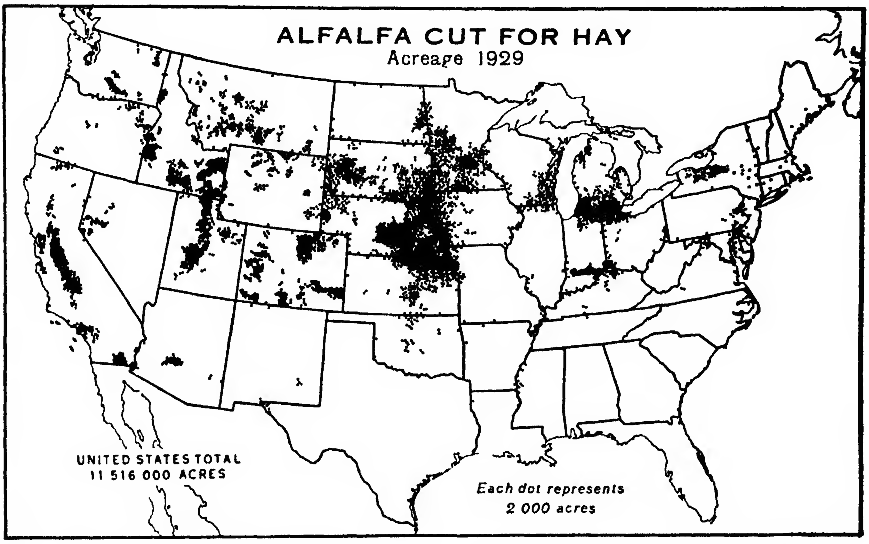

Figure 1.—Distribution of alfalfa production in the United States in 1929. Approximately 11,500,000 acres were cut for hay in that year.

Canadian borders and from the arid West to the humid East. They differ not only with respect to soil and climate, but also with respect to their resistance to disease and insect injury.

These differences, long recognized by alfalfa growers and research workers, are now being utilized by plant breeders as the basis of improvement of the crop, and the results of breeding work to date indicate that superior strains can be developed that will make possible an even greater use of alfalfa on the farms of America.

EARLY HISTORY

The best authorities agree that the original home of alfalfa was in southwestern Asia, from Mesopotamia northward across Persia and Turkistan to Siberia. De Candolle (*4*) states that it has been found wild, with every appearance of being an indigenous plant, in several provinces of Anatolia, to the south of the Caucasus, in several parts of Persia, in Afghanistan, in Baluchistan, and in Kashmir. More recently, Department of Agriculture explorers have found many so-called "wild alfalfas" in the region of Turkistan, so there can be no doubt that alfalfa got its start in this general region.

Alfalfa was probably planted in this region by half-civilized man ages before any history was written. The earliest records indicate that by that time man had discovered the superior feeding value and soil-building properties of alfalfa. One of the earliest Roman agricultural writers, Columella, stated in De Re Rustica, written about 56 A. D., that all emaciated cattle whatsoever grow fat on it and that it fertilizes the land.

Alfalfa was thus developed in dry regions and was usually found in river valleys with soils rich in lime and of alkaline reaction. Wing (*32*) has suggested that the grass eaten by Nebuchadnezzar when he was driven into the fields was none other than alfalfa growing in the fertile valley of the Euphrates River near Babylon. The earliest records alluding to alfalfa were discovered in Babylonian text written in 700 B. C. In this reference alfalfa is listed under its Persian name, aspasti, by the gardener of the Babylonian King, Mardukbalidin, which shows that alfalfa was known in the palace grounds of that day.

From this point on the story of alfalfa becomes history. Pliny and Strabo, both early Roman writers, record that when the Medes and Persians invaded Greece in 490 B. C , they introduced alfalfa into that country for the sustenance of their chariot horses, camels, and domestic animals. The plant was named medic, to denote its Median origin, and it has retained this root in the present botanical name, *Medicago*. This is believed to be the first introduction of alfalfa into Europe. From there it spread to Italy and during the next centuries to other European countries, including Spain. Thus the queen of forage plants, as it has been called, followed the path of historic civilizations and conquering armies from East to West.

Introduction into the Americas

The first introduction of alfalfa into the Americas was through the Spanish explorers. When Cortez and Pizarro had completed their conquest, the natives had alfalfa in lieu of their gold. This was at the beginning of the sixteenth century, and alfalfa soon became distributed over Peru and Chile. It is probable, though not certain, that some of the Catholic missionaries brought alfalfa from Mexico into southern California, New Mexico, and Arizona. Be that as it may, there was no decided spread of alfalfa growing in North America at this time.

The English, French, and Germans introduced alfalfa into the colonies of the Atlantic seaboard under the name of lucerne. There was some success in growing it in Virginia, North Carolina, Pennsylvania, and New York, but there were also some disappointments, due, no doubt, to a general lack of well-drained limestone soils and also to lack of knowledge of the necessity of inoculating for nitrogen-gathering bacteria, which, when present, grow on the roots of legumes. General Washington tried alfalfa at Mount Vernon with enough success to warrant planting a field of it in 1794. Thomas Jefferson, according to Spurrier, took considerable pride in his lucerne field, which was in production prior to 1793.

To trace the further introduction of alfalfa into the United States, it is necessary to return to the west coast, where in the gold rush days of the 1850's many prospectors came via the all-water route around the Horn to California. Some of them stopped at Chilean ports en

route, and, curious as to how this new plant would grow in the new country, took some seed with them. One of the first growers of alfalfa in California, according to the account related by E. J. Wickson to Wing, was W. A. Cameron, of Marysville, in the Sacramento Valley. He produced alfalfa in 1851, and his seed came from Chile.

From the beginning alfalfa produced remarkably good crops in the fertile irrigated valleys of California, and it is not strange that its gradual spread was across the oountry from the West rather than from the East, because, although it had been grown continuously in New York for over a century, it received its main impetus from the success it had attained in the West. From California it was soon taken to Utah, where the Mormons found it extremely satisfactory. It was then introduced into Colorado, Kansas, and Nebraska. According to the 1916 report of the Kansas State Board of Agriculture (*8, p. 11*), one of the first successful growers of alfalfa in Kansas was Charles J. Grosse, of Marion, who received his seed in 1868 from the Trumble Seed House on Sansom Street, San Francisco, Calif. In the 1890's alfalfa had become an important crop in Kansas and spread into Nebraska, where it was also successful. By 1900 it had crossed the Missouri River and become important on the well-drained and alluvial soils of Iowa and Missouri. Then it spread across the Mississippi into Illinois. Wing had previously carried the crop from a ranch in eastern Utah to Champaign County, Ohio, where he established one of the first really successful alfalfa projects in the State.

Considering the historical background of alfalfa production in this country, it is probably safe to assume that the so-called Common alfalfa now being extensively grown originated from the early introductions of Chilean alfalfa. It is also evident that through the years the crop has been remarkably changed by natural regional selection. As indicated by Westover (*30*), strains developed that have the ability to become relatively dormant in the fall and resist cold, as is the case with Northern Common. Other strains, such as the Common alfalfa found in the South, grow rapidly late in the fall; in other words, they do not respond so greatly to the shortening day length. Hybridization no doubt has also been a factor in this adaptation, but segregation by survival has been predominant.

Grimm Alfalfa

At about the time alfalfa was being introduced into California, another circumstance was paving the way for the growing of alfalfa in northern climates. In 1857 Wendelin Grimm brought his family from the Grand Duchy of Baden, Germany, to Carver County, Minn. (figs. 2 and 3). In the spring of 1858 he sowed 15 or 20 pounds of alfalfa seed brought from his native land. This proved to be the origin of what was later called Grimm alfalfa—the first alfalfa grown in this country that had sufficient hardiness to withstand the cold winters of the North. Many attempts had been made to grow the nonhardy alfalfas in Northern States, but this invariably resulted in winter-killing. The advent of Grimm alfalfa greatly increased the acreage importance of the crop.

There can be no doubt that the wide distribution of Grimm today is due to the comparative testing of experiment stations, where its

superiority was proved and given publicity. This alfalfa was grown in practical obscurity for almost 50 years before it came to the attention of experiment station officials, after which it was soon widely known. It would be hard to find a better example of the leadership afforded by experiment stations in agricultural work.

The discovery--and it can well be called a discovery, because very little was known regarding the adaptation of alfalfa in this early period—that certain strains were not adapted to certain regions while others thrived there, was an important one. No longer could a prospective grower just ask for alfalfa seed—he had to be sure of the kind of alfalfa seed he was getting. Some confusion thus arose because it was impossible to tell one variety from another by the seed, but fortunately this difficulty has been overcome by certification and verification services made available by State and Federal institutions.

Figure 2. Mr. and Mrs. Wendelin Grimm, of Chaska, Carver County, Minn. In 1858 Mr. Grimm planted 15 or 20 pounds of alfalfa seed he brought with him from Germany the previous year. This was the beginning of the present widely grown and popular Grimm alfalfa variety. (Courtesy of A. C. Arny, Minnesota Agricultural Experiment Station.)

Early Breeding Work

Without doubt, natural selection in alfalfa, helped here and there by the willing hand of man, has taken place for many generations. This is evident from a comparison of our vigorous-growing, sturdy cultivated alfalfas with the prostrate, slow-growing wild species picked up by plant explorers. But it must also be admitted that no plant of such economic value and antiquity shows so little evidence of deliberate breeding.

Only two examples, both cited by Brand (*2*), 1907, are needed to show what apparently had been accomplished by natural selection, helped along by man. Peruvian alfalfa, which is now grown to a considerable extent in the Southern States, has a very low zero point, that is, ability to grow at a low temperature, but is not at all winter-hardy in northern latitudes. This, Brand suggested, has been due to many centuries of growing in warm climates. On the other hand, it is

rather surprising that the original home of Grimm alfalfa in Germany has minimum temperatures less severe than those observed at Albuquerque, N. Mex. From all available records it is clear that the bulk of the original Grimm seed was not sufficiently winter-hardy for Minnesota conditions. Yet by saving seed from the plants that survived each successive winter, generation after generation, the persistent German immigrant, Wendelin Grimm, showed what could be accomplished in the way of acclimatization or adaptation of alfalfa in Minnesota.

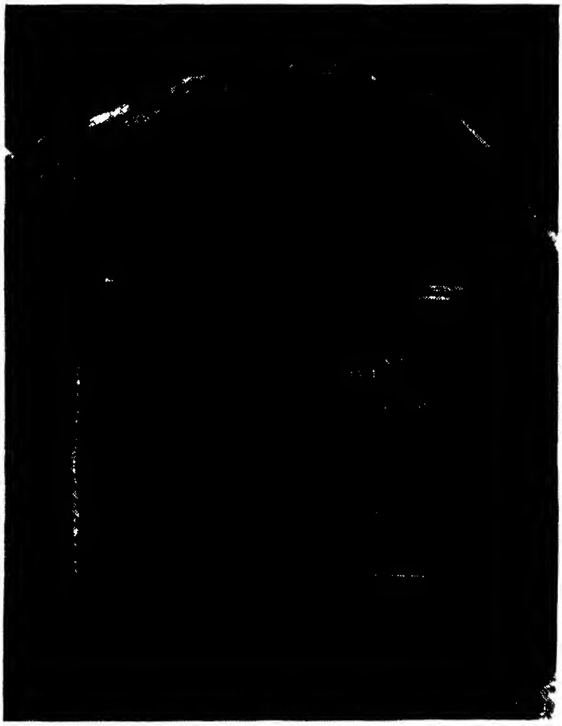

Figure 3.—Monument erected in honor of Wendelin Grimm, who greatly benefited northern agriculture by originating the hardy variety that bears his name. (Courtesy of A. C. Arny, Minnesota Agricultural Experiment Station.)

In a report of the committee for breeding forage crops, made by Piper (*24*) in 1909, a very good picture is given of the alfalfa-breeding program in the entire United States at that time. "It must be borne in mind", the report states, "that alfalfa breeding is a very recent development of plant improvement, apparently no work having been conducted along this line previous to 1903." At the time of the report 11 workers were directly interested in alfalfa improvement: J. M. Westgate, C. J. Brand, G. W. Oliver, and A. C. Dillman, all of the United States Department of Agriculture; G. F. Freeman, of Kansas; W. H. Olin and P. K. Blinn, of Colorado; F. A. Spragg, of Michigan; E. G. Montgomery, of Nebraska; W. A. Wheeler, of New York; and L. R. Waldron, of North Dakota.

Practically all these workers had a well-developed program, chiefly involving mass selection. Only Oliver, Westgate, and Brand report hybridization of varieties or species, but without definite results. Two rather distinct methods of selection were followed. Spragg, Dillman, and others selected mother plants without control of the male parent except cutting back adjacent undesirable material at the time of blooming. Olin, Oliver, Brand, and others self-fertilized the selected plants, using wire cages or bagging. This group thoroughly

understood the possibility of contamination by cross-fertilization, but apparently they did not fully realize that an individual selected plant might not necessarily—probably would not—pass on all its good characteristics to the next generation. Thus too much effort was often spent in picking out the best plant in the entire nursery, only to find when seed was obtained that the daughter plants were not at all like the mother plant. It must be added, however, that even at this early date many breeders knew the value of the progeny test and used it to determine which was the best parental material.

The workers of this period had a considerable number of strains to use for foundation stock. The State experiment stations had access to the collection of the Department of Agriculture, which included introductions from all important alfalfa-growing regions as well as material from more out-of-the-way parts of the world. The major varieties used were Grimm, Common, and Turkistan. There were also introductions of other species, chiefly *Medicago falcata* L., and a few species crosses were made, but apparently nothing came of them.

Among the more important characters selected for at this date were frost resistance, forage productivity, drought resistance, desirable habit of growth, seed productivity, leafiness, and resistance to leaf spot (*Pseudopeziza medicaginis* (Lib.) Sacc.). It is interesting to note, however, that only one worker mentions breeding for disease resistance, and then it is not given much prominence. In reply to the question "What are the most serious difficulties you have found in breeding alfalfa?", made in Piper's survey of 1909, the following answers were received:

(1) Difficulty of keeping strains pure, both during breeding and for increase.
(2) Maintaining a large nursery several seasons to await winter-killing or drought to eliminate undesirable individuals.
(3) Securing seed.
(4) Length of time required to determine the value of any given plant, some suggesting 3 years as the minimum.

Results of Early Improvement Work

The early work can be said to have begun about 1903 and ended about 1915. During this period there was considerable interest in the improvement of alfalfa, one outstanding character sought being winter-hardiness (fig. 4). A group of superior varieties and strains, together with the date they originated, is listed in the appendix, and it may be noted that several of these came into prominence during this early period, notably Grimm, Baltic, Cossack, Ontario Variegated, and Ladak. Figure 5 shows the origin of Ladak and the nursery from which it was selected at the United States Department of Agriculture Experiment Station, Redfield, S. Dak. All of these varieties have superior characteristics, such as cold resistance and adaptation for special conditions. They are all still considered standard varieties. Introduction and selection played a part in their development.

It must be added, however, that many an alfalfa selection was "born to blush unseen" during this period. Some very promising selections made in various nurseries never got any further. Wheeler's Grimm No. 19A was increased to the extent of 100 acres, then turned over to farmers and its identity lost. No doubt the worth-while

characteristics in this strain have through the years gradually made themselves felt in other strains with which it crossed. Thus the work put into such selections has not been entirely lost.

Nevertheless, the early work did not reach full fruition, for several reasons, among them the World War, which focused attention on the food crops to the detriment of the feed crops, and the widespread

Figure 4.—A demonstration of the difference in cold resistance of different alfalfas. Nebraska-grown Common alfalfa at left and Peruvian alfalfa at right, seeded May 16, 1922 Both varieties seemed equally good during 1923 and 1924, but the Peruvian winter-killed almost completely in the winter of 1924–25, while the Nebraska Common was uninjured Photographed May 25, 1925 (Courtesy of T. A. Kiesselbach, Nebraska Agricultural Experiment Station)

introduction of Grimm alfalfa, which largely solved the winter-hardiness problem, wiping out the advantage gained by selection for hardiness in Common alfalfa, and also depriving breeders of a definite goal for selection In other words, for the moment no great catastrophe threatened alfalfa, and most people, including the breeders, were content to let well enough alone

But events were already developing that brought a great revival of interest in the improvement of alfalfa and other forage crops.

New Problems Appear

Crowding into compact communities leads to peculiar problems with plants as with human beings Growers will tell you they can remember when they could plant alfalfa and leave it down almost any number of years without any trouble This cannot be done any longer. The problem of winter hardiness was largely overcome by the general use of Grimm and other cold-resistant varieties, but

another major problem appeared and became increasingly insistent. It manifested itself in the killing out of stands after 2, 3, or 4 years of production. No one knew what was causing the trouble. Finally it became so serious that Department of Agriculture workers undertook to determine the underlying cause.

Finally Jones and McCulloch (*15*) found the disease was produced by a hitherto unknown organism, a bacterium to which was given the

Figure 5.—The original alfalfa nursery at Redfield, S. Dak., from which Ladak was selected. The seed was sent to the United States Department of Agriculture from the Province of Ladakh, in northern India, in 1910 and was planted in 1914. Photographed July 20, 1915. The entire acreage of the Ladak variety now being grown in the United States came originally from the two rows marked by the arrow. The light color of the rows is caused by the profuse bloom, the preponderance of which was yellow in color. (Courtesy of S. Garver.)

name *Aplanobacter insidiosum* McCulloch, the insidious *Aplanobacter*, more recently changed to *Phytomonas insidiosa* (McCulloch) Bergey et al. The disease it caused was called bacterial wilt. Since its discovery in 1925, apparently increasing inroads have been made by the disease until at the present time it is known to occur from the Atlantic to the Pacific and from the Northern States to the southwestern border. It was apparently most severe in the river valleys of Nebraska and Kansas at first, but it is now found in considerable abundance eastward through Iowa, Illinois, Indiana, Michigan, Ohio, Wisconsin, and other States.

Of the approximately 11½ million acres of alfalfa harvested for hay in the United States in 1934, the 1934 census shows that over 7½ million acres were grown in the 14 North Central States bounded on the east by Ohio and on the west by Colorado. At the present time bacterial wilt is prevalent throughout this region, although it is more serious in some localities than in others. In this region, too, alfalfa is usually allowed to remain as long as there is a good stand. When it kills out it must be plowed and another field planted to maintain a hay balance. The available domestic alfalfas such as Grimm, Hardigan, and Common are very susceptible to the bacterial wilt disease

and kill out, where the disease is severe, in from 2 to 4 years. Figure 6 shows the ravages of bacterial wilt in the domestic varieties in field plots at the Kansas Agricultural Experiment Station.

Bacterial wilt annually destroys hundreds of thousands of acres of alfalfa, with aggregate losses equivalent to those that would be experienced by farmers as a result of flood, drought, or any other major disaster. These losses include not only the crop destroyed by the

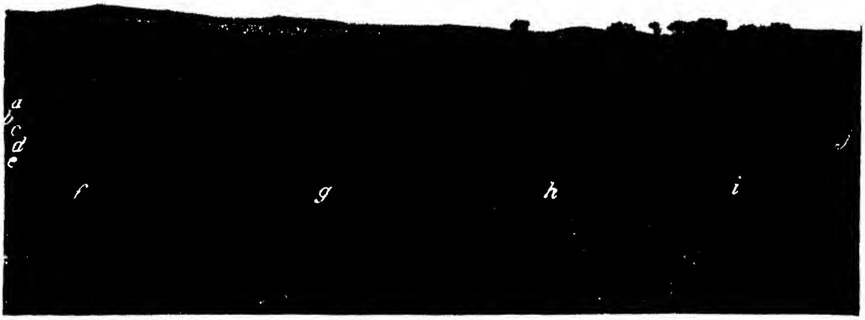

Figure 6.—Experimental plots at the Kansas Agricultural Experiment Station, Manhattan, Kans., demonstrating resistance or lack of resistance of different varieties to bacterial wilt, the plots with a poor stand being covered with weeds. *a*, Kansas Common (poor stand); *b*, Turkistan F. C. 19303 (good stand); *c*, Turkistan F. C. 19304 (good stand); *d*, Grimm (poor stand); *e*, Ukranian F. C. 19315 (poor stand); *f*, Turkistan F. C. 19316 (good stand); *g*, Kansas 308—a resistant selection from Kansas Common (good stand); *h*, Dakota Common F. C. 16081 (poor stand); *i*, Argentine F. C. 15996 (poor stand); *j*, Cossack F. C. 18836 (fair stand). These plots were planted in the fall of 1930: photographed September 1936. The greatest decrease in stand took place during the third and fourth years. (Courtesy of C. O. Grandfield, Kansas Agricultural Experiment Station.)

disease but also the cost of seeding and the loss of production from the land until a new crop is established. If, through the use of resistant strains, growers could maintain stands of alfalfa for even 2 years longer, they would be able to save millions of dollars.

Considerable preliminary work indicated that cultural practices in general would not control the disease. The only avenue of approach that offered possibilities was a breeding program. For a number of years Westover and his coworkers, plant explorers of the Department of Agriculture, have been gathering alfalfas from remote parts of the globe. This collection has progressed until at the present time approximately 1,000 different strains of alfalfa are growing in various nurseries in the United States. Some of these were gathered in areas where the natives had never seen or heard of an automobile. Of the alfalfa strains tested from every continent, and almost every country, practically the only strains having decided resistance to bacterial wilt have been found in the region around Russian Turkistan, northern India, western China, and northeastern Persia. Even some alfalfas

of the wild type and the *Medicago falcata* strains found in this region have shown resistance to bacterial wilt. The objective of the breeding program, then, is to combine the good qualities of commercial alfalfas such as Grimm and Common with the bacterial wilt resistance found in the Turkistan alfalfa.

PRESENT ALFALFA IMPROVEMENT WORK

As already indicated, both new problems and new advances in plant breeding have greatly stimulated alfalfa improvement. At the present time a relatively large number of breeding projects are being started or have recently been started, and there is a great deal of interest on the part of almost all experiment stations, whether or not they are themselves actively engaged in alfalfa-improvement work. In order to make the present status of alfalfa improvement clear, the work that has already been done both in the United States and abroad will be briefly summarized.

Correlation of Characters

When selection is desired for a certain character, it is often desirable to determine, if possible, what other characters of the plant are associated with it. Sometimes certain characters are inherited together. By selecting for one, it may then be possible to secure the other also. This association of characters frequently presents difficulties. In alfalfa, for example, selection for increased forage production usually gives at the same time a more coarse, sparsely leaved plant of poorer quality. In 1914 Freeman (*11*) published a paper of interest from the standpoint of selection of material. He studied correlations between various characters in alfalfa and, among others, found positive correlations indicating that nitrogen content is associated with the percentage of leaves, and green weight with both the average number of stems and the average height. He found negative correlations indicating that greater forage yield is associated with smaller percentage of leaves; smaller percentage of leaves with greater height; smaller number of stems with greater average height. There was no significant correlation between thickness of stand and percentage of leaves.[3] Freeman concludes (*11, p. 367*):

> In economic plant breeding one frequently encounters physiologically negative correlations such as those, in alfalfa, between height and stooling capacity, height and percentage of leaves, and between yield and quality. In seeking improvement, therefore, the breeder must recognize and make use of these facts in the interpretation of results obtained, and also search for races which violate such naturally antagonistic correlations to the greatest possible extent.

Hackbarth and Ufer (*13*) found a relatively high positive correlation between forage yield and height[4] and also a positive correlation between height of stem and length of internode and coarseness of stem.

---

[3]	*r*
Correlation between nitrogen content and percent leaves	0.60±0.06
Correlation between percentage of leaves and thickness of stand	.05± .10
Correlation between percentage of leaves and forage yield	−.39± .09
Correlation between percentage of leaves and height (height 27 to 32 inches)	−.58± .06
Correlation between green weight and average number of stems	.57± .07
Correlation between green weight and average height	.25± .09
Correlation between average height and number of stems	−.25± .09
Correlation between average height and percent leaves	−.40± .09

[4] $r=0.851$.

Thus high-yielding plants were tall and upright but of low quality because they had long internodes, were sparsely leaved, and had thick, woody stems. They suggest, however, that the correlation is not absolute and that with a sufficiently large number of plants to choose from it might be possible to obtain the desired combination of height and quality. Of especial interest is the finding of a positive though slight correlation [5] between forage production and seed production. Since it is considered by many that high forage yield militates against high seed yield, it is noteworthy that they found a number of lines (clones) in which high yield of forage was associated with high seed production. Fleischmann (*10*) has also found strains that combine relatively high forage and seed yield. In this connection Helmbold (*14*) has found some correlation between the following characteristics and high seed production, and selection for these characteristics may help attain the desired end:

(1) A definite (closed) blooming period.
(2) Large flower clusters.
(3) Great individual ability to set seed. (He believes the female parent has a greater bearing on seed productivity than the male)
(4) Many coils per pod with high seed number per pod.
(5) Least possible shattering of seed.

Other workers, including Kiesselbach and Anderson in Nebraska and Willard in Ohio, have also found a very high correlation between nitrogen content and percentage of leaves. Thus it seems evident that for a higher quality crop it is necessary to have a high percentage of leaves and also that the plant retain those leaves until harvest. Thus disease resistance as well as inherent leafiness is involved, because most of the leaf-spot diseases, for example, tend to defoliate the plant.

Hybrid Vigor

The question of how much crossing naturally occurs in alfalfa brings such different answers that there is obviously no exact information on the point. Waldron found 42.7 percent crossing between purple and yellow, the yellow being the female parent, while he found 7.5 percent crossing in the reciprocal, the purple being the female parent. As high as 80 percent crossing has been observed in Nebraska between closely associated plants of the purple-flowered (*Medicago sativa*) and yellow-flowered (*M. falcata*) alfalfa, the female again being yellow. It is more difficult to determine the crossing between purple-flowered strains of similar origin because of the difficulty of determining when a cross is obtained. This difficulty is now being overcome in the production of "testers" by at least three experiment stations. These include a strain produced by the South Dakota station with pure white flowers, the character acting as a simple recessive. Another strain produced at the Wisconsin station has red roots, also simply inherited; and the Nebraska station has a strain producing four or five leaflets instead of the usual three. These strains all have the *M. sativa* type of flower, and by their use reliable information should be obtained on the amount of natural crossing, the distance necessary for isolation, and possibly on the activities of various insects.

[5] $r=0.202$

A considerable body of facts bearing on the question of the influence of self-fertilization on an alfalfa population is gradually being established. The work of Kirk (*17*), Williams (*31*), Torssell (*26*), Dann (*7*), and others suggests, on the whole, decrease in productivity of both forage and seed yield when plants are self-fertilized. The decrease is very marked in most cases; for example, Williams (*31*) reports that 14 parent plants produced an average of 2,433 seed per plant, while the average yield of the first-generation selfed progeny was only 301 seeds. Kirk found that the first generation selfed produced only 62 percent as much as the cross-fertilized parent, and the second selfed generation only 30 percent as much as the original parents.

The German workers, including Dann (*7*), also found a decided decrease in seed production with self-fertilization as compared with cross-fertilization. Helmbold (*14*) found that crossing gave a higher percentage of pods than selfing. By crossing with foreign pollen, 24.86 percent of the flowers formed pods. With close pollination (pollen from the same plant but different flowers) 18.26 percent formed pods, and with strict selfing 17.54 percent formed pods. Crossing also gave the highest number of seeds per pod, an average of 2.34, while inbreeding gave the least, an average of 1.38 seeds per pod. Most workers agree that there is no self-sterility, in the true sense, in *Medicago sativa* or *M. falcata*.

Tysdal and Clark (*27*) found decided decreases of seed production in self-fertilized lines as a general rule, but point out several instances where selection for seed productivity increased production, particularly in Turkistan lines, which as a rule are naturally low in seed yield. These lines were carried into the fourth generation of selfing and represent a decided improvement in the inherent ability to set seed over the original parent. Kirk (*18*) has isolated a strain of alfalfa during the course of his breeding work that he characterizes as "autogamous", that is, it is extremely self-fertile and sets seed readily without manipulation.

The seed production resulting from hybridization compared to that of the original parental stock has not been so carefully worked out. It is evident that open pollination or cross-pollination between selfed lines brings them up nearly to parity with the open-pollinated parents, but there are very few definite examples, if any, of large increases attributable to hybrid vigor. Most of the comparisons have been with the progeny of self-fertilized individuals and not with the original parent, and the relative improvement in the cross is therefore difficult to determine. Carlson (*5*) found decided decrease in seed production upon self-fertilization, and then when open pollination—with no way to determine the amount of crossing—was allowed, seed production increased over that of self-pollination but still did not reach that of the open-pollinated parents. In the work reported up to the present time it has not been possible to recombine desirable inbred strains with the object of producing a superior first-generation hybrid, as is being done with corn, because such inbred strains were not available; but at present there are a number of lines that have superior germ plasm with respect to seed production as well as other desirable characters.

The available data on the influence of self-and cross-fertilization on forage production somewhat parallel those on seed production. Kirk (*16*) found the following percentages of forage yields: Cross-fertilized, 100; first generation selfed, 81; second generation selfed, 72; third generation selfed, 53 (fig. 7); but he also found certain second-and third-generation selfed lines that produced 100 percent or more as

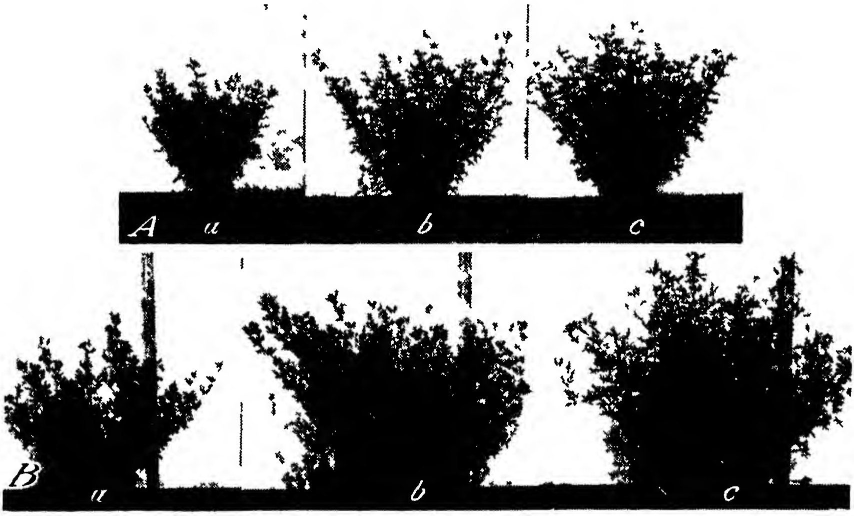

Figure 7—*A*, Representative alfalfa plants from strain no 22, showing reduction in vigor due to self-fertilization *a*, Open-fertilized, *b*, first generation selfed, *c*, second generation selfed *B*, Representative alfalfa plants from strain no 3, showing reduction in vigor due to self-fertilization *a*, Open-fertilized, *b*, first generation selfed; *c*, second generation selfed (Courtesy of L. F Kirk, Dominion Agrostologist, Ottawa, Canada.)

compared with the original parent This coincides in general with results of other workers, there being not such a very great decrease in forage production of some lines, and a tremendous variability with respect to the reaction of different lines—some showing great loss of vigor, while others show very much less. It must be admitted, however, that the chance of obtaining a superior forage-yielding strain of alfalfa by self-fertilization appears rather remote at the present time

As in the case of seed production, most of the comparisons in forage production are between open- and self-pollinated lines. Waldron (*29*), however, as far back as 1920 pointed out hybrid vigor in crosses between two alfalfa species He allowed natural crossing to take place between *Medicago sativa* and *M. falcata* Subsequently he obtained yield data from the first-generation-hybrid individuals compared with other individuals produced by normal pollination within the species He found an increase in forage yield of 51 percent of the *M. sativa* × the *M. falcata* hybrids over the pure *M. sativa,* and 43 percent increase of the *M falcata* × *M sativa* hybrids over the pure *M. falcata.*

This is an interesting observation, particularly in view of the fact that the most widely cultivated alfalfas, in both Europe and North America, are considered to be the result of a natural cross between these two species. Thus without knowing it commercial growers are probably taking advantage of hybrid vigor. In a study of the variegation in flower color of 64 strains and varieties of European alfalfa, Waldron (*28*) found only 5 that did not show any variegation, and 3 of these were Turkistan. Hembold (*14*) states that in his opinion the appearance of any color but pure purple in the flower surely indicates foreign crossing in the *M. sativa* group, and as a rule the introduction of *M. falcata* blood.

The general results of inbreeding and crossing in alfalfa point to the strong possibility of hybrid vigor being obtained for forage yield if the proper combinations of lines are made. The results also point to the possibility of using species crosses to effect improvement. In a later paragraph more information is given on various species that may have possibilities for crossing.

Progress in Selection for Disease and Cold Resistance

In the replies from questionnaires sent to practically all alfalfa workers in the world in connection with this survey, many indicated that they were selecting for cold resistance and others that they were selecting for both cold and disease resistance. In the past Grimm alfalfa was an outstanding example of natural selection for cold resistance. The introduction of various lots of seed and subsequent selection and increase, as in the case of Cossack, Ladak, and other varieties, resulted in the production of additional material of high cold resistance.

In many projects selection is being carried on with the object of purifying strains and making them homozygous for certain characteristics, then recombining the lines to form new varieties. Such work has advanced to the point where some information has been obtained on the breeding behavior of lines, but very little on the behavior of the recombinations.

As a result of a study of the reaction of selfed lines to cold, Kirk (*16, p. 15*) states:

> Inheritance has clearly played an important part and segregation into hardy and non-hardy lines is plainly indicated in the second generation of self-fertilization. Strains IV and VII may be cited as obvious cases in which lack of hardiness has been transmitted in some degree from one generation to another. In one second generation line of strain IV, every plant was winter killed. [The cross-fertilized parental stock of strain IV winter-killed 28 percent.] Lines III and XIII are notable illustrations of segregation in the second generation of selfing for hardy and non-hardy families of plants.
>
> In striking contrast to the strains in which inherent nonhardiness made an appearance are * * * strains * * * in which practically no winter-killing occurred.

Waldron (*28*) found segregation for cold resistance with one generation of selfing, and he also obtained increased cold resistance by selection of mother plants—indicating a great heterozygosity or mixture of inheritance in individuals with respect to this characteristic.

A number of superior lines have been segregated by various workers in the United States. Wisconsin, Kansas, New Jersey, Michigan, and

Nebraska have had rather intensive improvement programs under way, and progress is reported in fixing desirable characters such as cold and bacterial wilt resistance in certain lines. Peltier and Tysdal (*23*) report that selfing alfalfa through the fifth generation has increased the homozygosity for bacterial wilt resistance—that is, a larger and larger percentage of the plants were resistant—provided selection for this character was carried on during the inbreeding process. If no selection for disease resistance was practiced during the inbreeding process, a rather marked decrease in bacterial wilt resistance occurred from generation to generation, although some few lines were consistently high in bacterial wilt resistance. Practically the same results were obtained with cold resistance. Selfing without rigid selection for cold resistance and elimination of the cold-susceptible individuals resulted in a marked decrease in resistance, taking the population as a whole. There was, however, great variation and segregation in different lines, as has been found by other workers. Thus, when the cold-resistant segregations were selected by means of artificially controlled freezing tests, the cold resistance of superior lines was maintained in spite of self-fertilization. It was also found possible to obtain high bacterial wilt and cold resistance either in the same lines or independently, thus indicating independent inheritance. Figure 8 shows two hybrids relatively resistant to bacterial wilt, as compared with the bacterial wilt-susceptible Grimm variety.

Brink, Jones, and Albrecht (*3*) at the Wisconsin station report segregation for bacterial wilt resistance in selfed lines from Hardistan alfalfa, some having a very high degree of bacterial wilt resistance. They state (*3, p. 642*): "Resistance to bacterial wilt in alfalfa behaves in inheritance as an intergrading character and probably rests upon a complex genetic basis. A factorial interpretation is at present impossible."

In certain crosses between resistant and susceptible lines the same workers found varying percentages of resistant offspring. In the case of a Turkistan × Hairy Peruvian cross, 58 percent of the second-generation offspring were resistant, while a Turkistan × Grimm cross gave relatively few resistant segregates.

Thus while complete success has not yet been attained in the fight against winter hazards and disease, it is safe to say that remarkable progress has been made in obtaining lines that are superior in these characters. These lines contain the necessary genetic stability for these characters, and the next step will be to combine them to produce a variety with as much bacterial wilt resistance as is now found in any commercial variety, or even more, together with such desirable characters as high forage and seed yield, freedom from leaf diseases, and other attributes. To say that this is an easy task is to underestimate the difficulty of the problem and the whims and caprices of nature.

In the alfalfa-improvement work, the Department of Agriculture is cooperating with a number of State stations, among which the work in Kansas, Wisconsin, and Nebraska has been longest in progress. At each of these institutions superior strains are now available, some strains having more than twice the bacterial wilt resistance of the best commercial varieties. The Wisconsin station reports that among its

most promising material are lines having very high cold resistance selected out of hardy varieties, and also some bacterial wilt resistance found in occasional plants from well-known and highly susceptible American varieties. The Kansas station has also reported increasing the bacterial resistance by selection in the Kansas Common strain. The Nebraska station has promising lines developed from plant

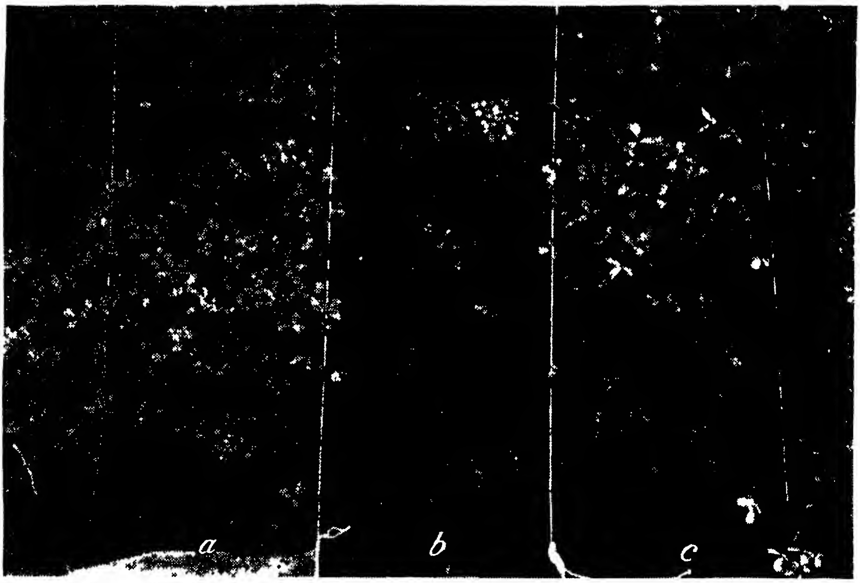

Figure 8.—Looking down on three strains of alfalfa artificially inoculated with the bacteria causing alfalfa bacterial wilt, grown in the Nebraska Agricultural Experiment Station greenhouse: *a*, Cross between a bacterial wilt-resistant Turkistan selection and *Medicago falcata*; *b*, Grimm (originally a natural cross between *M. sativa* and *M. falcata*); *c*, a cross between bacterial wilt-resistant selections from Turkistan and Ladak. All three had an equal number of plants when inoculated, but Grimm has been almost completely killed by the disease, while the two resistant crosses maintain a stand. (Photographed 4 months after inoculation.)

selections from old fields of the State, foreign introductions, and the Ladak and Cossack varieties.

The New Jersey station has had selection and hybridization in progress for some time and reports the possibility of selection for a type of root resistant to heaving, as well as selection for adaptation to particular soil conditions.

Various stations now also have access to strains with rhizomes or underground stems. These are particularly interesting from the standpoint of pasture types and erosion control, as they form a matted growth and bind the soil.

Relation of Insects to Alfalfa Improvement

There is some division of opinion, but in the main considerable agreement, regarding the kinds of insects that assist seed setting in alfalfa. Practically all workers agree that the leaf cutter bees (*Megachile* spp.)

are very effective in causing tripping or forcing of the pistil out of the keel. Piper et al. (*25*) found the bumblebee (*Bombus* spp.) to also be fairly effective for tripping. They found that butterflies caused practically no tripping, and this was true also for moths and other night-flying insects. The ability of the honey bee (*Apis mellifera* L.) to trip alfalfa flowers is not so easily clarified. Piper et al. found that honey bees tripped only from 0.3 to 4.7 percent of the flowers visited and many visits to the flower were required before tripping was effected. Dwyer (*9*), of Australia, has found that honey bees cause a considerable amount of tripping and has suggested the use of honey bees in cages in breeding work. Michigan workers have also found the honey bee to be effective when confined to small areas. Helmbold (*14*) states that honey bees collecting pollen cause tripping and attributes more tripping to them than to bumblebees. He also says that the following bees are effective in tripping alfalfa flowers: *Macropis labiata* F. (female), *Melitta leporina* Panz., and *Anthophora bimaculata* Panz.

There is no doubt from the work of numerous investigators that insect visitation under most conditions will improve seed production, and it is probable that insects can be used to advantage for controlled pollination in certain breeding and improvement work.

There is some evidence that progress can be made in selecting lines resistant to harmful insects. Painter and Grandfield in Kansas have selected individual plants that are much more resistant to aphids (*Illinoia pisi* Kalt.) than the average of the variety. Some workers have also found individual plants that seem to carry resistance to leafhoppers (*Empoasca* spp.). At present these represent only possibilities in superior germ plasm. Insects that harm alfalfa from the standpoint of seed production, upon which little or no selection for resistance has been done, include the clover seed chalcid (*Bruchophagus gibbus* Boh.), certain species of bugs of the genus *Lygus*, and Say's stinkbug (*Chlorochroa sayi* Stål).

The Alfalfa Improvement Conference

In June 1934 a meeting of 27 alfalfa workers from 7 States and the District of Columbia was held at Lincoln, Nebr., and at this meeting attention was given to the formation of an informal association for the benefit of all workers interested in alfalfa improvement. In order to get the reaction of the eastern men it was decided to call another meeting to be held in connection with the American Society of Agronomy meeting at Washington, D. C., in November 1934. Nineteen States, the District of Columbia, and Canada were represented by 54 workers. After a thorough discussion a committee of five was appointed, composed of H. L. Westover, R. A. Brink, T. A. Kiesselbach, D. W. Robertson, and H. B. Sprague, to develop plans and methods for a permanent alfalfa improvement conference. This committee called a meeting of all interested workers to be held in connection with the meeting of the Corn Belt section of the American Society of Agronomy at St. Paul, Minn., June 1935, at which time final organization of the conference took place. At this meeting, representing 15 States and the District of Columbia, with an attendance of 78 workers, the following motion was adopted:

That the guidance of the Alfalfa Improvement Conference be in the hands of an executive committee of five, consisting of H. L. Westover, permanent secretary, and four additional members, one of whom would be chairman, to be elected biennially at the conference to be held in conjunction with the Chicago meeting of the American Society of Agronomy; and that summer conferences be held in alternate years at an experiment station where alfalfa investigations are in progress, the time and place to be determined by the committee.

The following were elected as members of the executive committee to serve until the fall of 1937: R. A. Brink, chairman; T. A. Kiesselbach, H. B. Sprague, and D. W. Robertson. In Mr. Westover's absence on plant exploration trips, H. M. Tysdal has been acting secretary.

Since its inception and organization the Alfalfa Improvement Conference has been active in disseminating information on progress in alfalfa breeding, has taken an active interest in plans for seed increase of desirable improved strains under isolation, has assisted in the exchange of breeding material, and at the biennial summer meeting held at Madison, Wis., in June 1936, laid the foundation of a cooperative program of testing new strains. In this cooperative testing two types of nurseries will be used—(1), an "observation" nursery composed of duplicate rod rows with appropriate standard checks, and (2), an advanced nursery composed of perhaps five or six replications of multiple-row plots. Yields will be taken on the latter nurseries, and also, where possible, on the former.

It is planned to have a considerable number of observation nurseries scattered throughout the country so that experiment station workers will have an opportunity of testing out the available new strains for their own conditions, and this will enable them subsequently to make intelligent varietal recommendations to alfalfa growers of their own States. The advanced nurseries will be located in representative areas to test out any definite regional adaptations that are found in the improved strains. One or more tests are also contemplated in a recognized alfalfa seed producing section to test this character. In addition to these cooperative field tests, attempts will be made to include testing under controlled conditions for such characters as resistance to diseases, to insect pests, and to low temperatures.

The Alfalfa Improvement Conference has already proved itself to be a vital force in coordinating the alfalfa improvement work of the United States. Reports of the conferences already held may be obtained from the Division of Forage Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture, Washington D. C.

Methods and Objectives of Present-Day Alfalfa Improvement

Even the most optimistic workers fail to see how it would be possible to produce one variety of alfalfa that would be the best for all sections of the country. Some workers, however, recognize a need for the development of strains of alfalfa especially suited to at least four general regions: (1) The northwestern region, north of the southern boundary of Nebraska and west of the eastern boundaries of North Dakota and South Dakota; (2) the northeastern region, which may roughly be designated as the area bounded on the west by the western boundaries of Minnesota and Iowa and on the south

by a line representing approximately the southern boundary of Pennsylvania; (3) in the middle region, including Kansas and Oklahoma and the surrounding territory eastward and westward; (4) the southwestern region, including southwestern Texas, southern New Mexico, Arizona, most of California, and the extreme southern parts of the United States along the Gulf of Mexico.

In regions 1 and 2 it is essential to have an alfalfa of high cold resistance. Bacterial wilt can also be found throughout these regions, but it is severe only in those areas where moisture and other conditions are favorable; it is not serious as yet in the dry-land areas or in the eastern regions where short rotations are the rule. However, it causes severe damage in parts of Ohio, New Jersey, and other Eastern States. The chief difference between the requirements for regions 1 and 2 relate to resistance to various leaf spots, particularly the leaf spot caused by *Pseudopeziza medicaginis* (Lib.) Sacc. and leaf blotch (*Pyrenopeziza medicaginis* Fckl.), and also to dormancy habits and resistance to potato leafhopper yellows. Cold-resistant Turkistan alfalfa has been fairly successful in region 1 but not in region 2, chiefly because of its susceptibility to leaf spots and the fact that in some cases its slow recovery after cutting allows grasses to encroach. At one experiment station in the Union of Soviet Socialist Republics, selections less susceptible to leaf spot have already been made, and it does not appear impossible that eventually a strain can be produced that will combine the qualities necessary for adaptability to both regions, 1 and 2. This would be all the more desirable because seed is often produced in the western area to be used in the eastern area. Also there is some evidence indicating an increase in the severity of bacterial wilt in eastern States, which would make bacterial wilt resistance desirable for this region.

In region 3, cold resistance is a less important factor, but it can by no means be entirely neglected. Bacterial wilt resistance is desirable if not necessary for many areas, and it seems probable that if a strain can be produced combining bacterial wilt resistance and the desirable habit of growth of Kansas Common alfalfa, it will be very well adapted for this region.

In region 4 the climate is so mild that cold resistance need not be considered, although there is apparently considerable difference in ability of the foliage of different strains to resist frost, and it is desirable to select for this character. Since tests have shown that the nonhardy alfalfas grow more rapidly and give better yields of hay in this region, selection work can be confined largely to southern types. Bacterial wilt has not been important in this region, although it has been found. Fortunately certain Persian introductions of the nondormant type have shown some bacterial wilt resistance and these are available for selection and breeding work for the region.

It is apparent from the foregoing that a large amount of selection and recombination of characters must be accomplished before the desirable alfalfas are obtained. Fortunately much of the foundation stock, including lines of high resistance to certain diseases and to cold, is already available. A cooperative arrangement with the various States to give accurate information on the adaptation of all new strains produced is now available under the auspices of the Alfalfa Improvement Conference.

The ultimate objective will be the combination of as many desirable characters in a single individual strain as possible. Most plant breeders constantly bear in mind and guard against the possibility that selection for one character, such as bacterial wilt resistance, may actually lead to the development or retention of characters undesirable in other respects For example, bacterial wilt resistance can readily be ob-

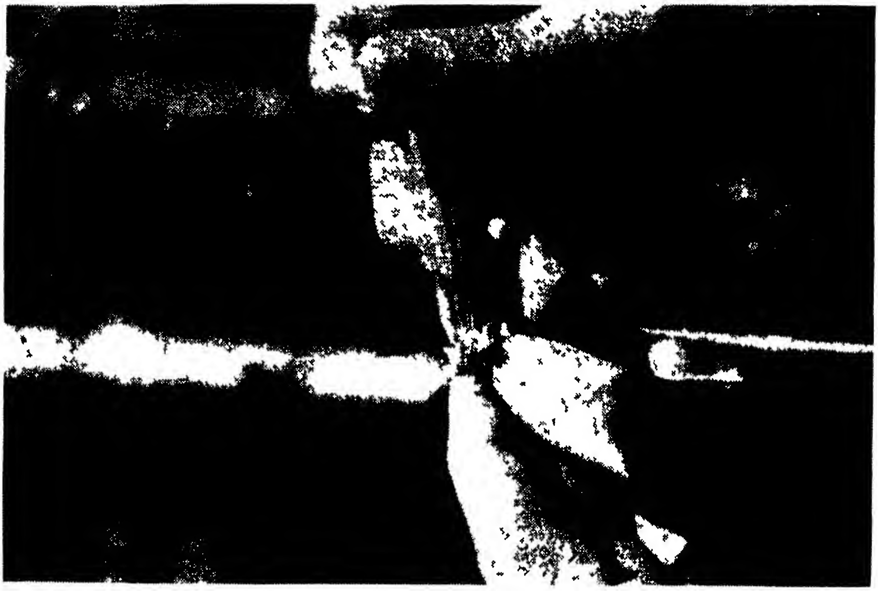

Figure 9—Emasculation of alfalfa flowers by suction. The glass tube is held over the stigma and stamens, and the suction (in this instance supplied by a rubber tube connected to the intake manifold of an automobile) removes the anthers and pollen. If all the pollen is not removed, a jet of water is applied to the stigma and suction finally removes all trace of pollen.

tained in Turkistan lines, but the strain is still undesirable because of other characters, including high susceptibility to leaf diseases.

Naturally present-day alfalfa breeders use a wide variety of methods in attacking the problem of improvement, although the underlying principles are the same. In hybridization work where emasculation is desired most American workers use the suction method or a combination of suction with a jet of water directed on the stigma. The suction method operates on the principle of a vacuum cleaner and is illustrated in figure 9.

It has been found advantageous not to allow the stigma to strike the standard or any other object when it is tripped or forced out of the keel for emasculation. It has also been found that in general it is unnecessary to emasculate the flower at a very early stage; emasculation is usually delayed until full bloom, even though the anthers have become ripe. If the pollen is carefully removed, apparently there is little danger of self-fertilization, and foreign pollen can then be applied immediately.

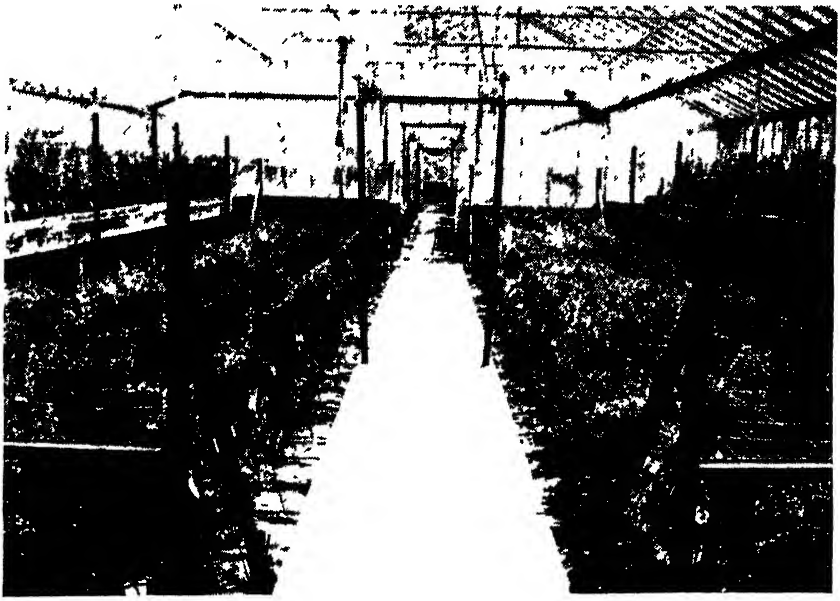

Figure 10.—Increase of seed of selected lines of alfalfa in the greenhouse at the Nebraska Agricultural Experiment Station. The greenhouse is screened against insects, and the flowers are tripped by hand, insuring self-pollination. Good seed setting can usually be obtained in the greenhouse even in unfavorable seasons, although temperatures often reach 120° F. inside.

Figure 11.—Seed increase of a selected alfalfa strain in an isolated block. Such a plot must be separated from any other by at least 20 rods; in this case the separation was about a quarter of a mile. The plants were transplanted to irrigated land in western Nebraska in the spring of 1936 from seedlings started at the United States Yuma Field Station, Bard, Calif., in December 1935. These plants produced a fair amount of seed the first year. The plot is surrounded by corn and sugar beets.

Selfing is accomplished by the use of bags, screen cages, or screened greenhouses, the flowers usually being artificially tripped, although not always. Some strains have been produced that set seed without any manipulation of the flower. Figures 10, 11, and 12 show some of the ways in which the problem of seed increase of selected lines is being met.

Perhaps of greater interest than details of technique are the principles followed in the breeding program itself. Some workers allow open-

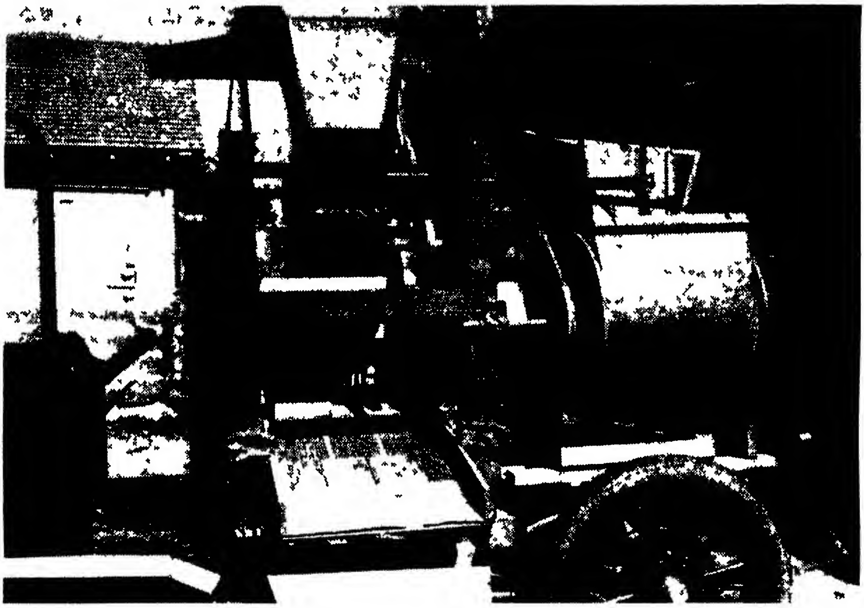

Figure 12.—Small, portable thresher for threshing both single plants and increase blocks of alfalfa. The single-plant material is run only over the rubber drum with apron shown at the right, while larger quantities are put through the cylinder, and pods that are not threshed fall through the screen and are then run over the rubber drum, which rubs all the seed out. The rubber drum is powered through an automobile transmission so the drum can be stopped when not in use, even though the cylinder is going. The whole machine is mounted on the chassis of a car, and the motor of the car used as power. This thresher has proved very satisfactory for relatively small lots.

fertilization in the nursery and select the best individual lines for propagation, while others employ strict inbreeding methods with the object of more rapidly fixing the characters desired and then recombining if necessary. Still others use a combination of these methods. Without doubt many alfalfa breeders are using the same method that has produced such remarkable results in hybrid corn, as described by Merle T. Jenkins in the 1936 Yearbook of Agriculture.

The problem of how to determine which lines when crossed will produce a superior hybrid is of great interest to alfalfa workers. At present the only way to find out is to try the lines in actual crosses, and it is difficult to make as many crosses as are necessary to test all

combinations. Corn workers use the top-cross method rather extensively at the present time for eliminating undesirable strains, and it has been suggested that a modified application of the same principle may be useful in alfalfa.

Evidence seems to indicate that long-continued inbreeding is not necessary to fix desired characters sufficiently for practical breeding purposes. If this is true a great deal of labor and time will be saved and also a larger number of lines can be produced and tested.

The backcross method or its modifications, as, for example, Richey's "convergent improvement" method, is apparently not very much used with alfalfa. Some type of backcross may be useful in such a problem as combining the bacterial wilt resistance of Turkistan selections with the desirable characters of Grimm, Cossack, or Hardigan. The application of the backcross method is not simple when the inheritance of resistance is complex, as is apparently the case with bacterial wilt, but the method should not be overlooked when it is yielding results in various other crops.

To obtain further information on the present status of alfalfa improvement, questionnaires were sent to all experiment stations in the United States and all foreign workers of whom there was a record. Among 40 replies, 23, representing opinions from England, Germany, Australia, and Canada, as well as the United States, indicated that alfalfa breeding or improvement work was in progress. In the replies to the question "What are the objectives in your selection or hybridization work?" the following objectives were mentioned the number of times shown:

Increased seed-setting capacity	10
Higher yield of good quality forage	8
Winter hardiness	8
Disease resistance	8
A type suitable for grazing	5
Adaptation to different soil conditions	4
Resistance to heaving injury	2
Insect resistance	2
Increase resistance to drought	2
Increase in protein content and leaf percentage	2
A type less susceptible to injury from early cutting	1
Larger seed	1

It is interesting to compare these replies with those obtained in 1934, given in the supplement to the Report of the Second Alfalfa Improvement Conference. The most significant change is found in the increased number of workers at present interested in selection for a pasture type of alfalfa for grazing, and also the increased number interested in selection for soil adaptation. This undoubtedly indicates a trend toward the increased use of alfalfa for grazing and a desire to use it on land to which it is at present not well adapted.

In the same questionnaire, in answer to the question "What problems and material need future attention?" the replies indicated further studies would be desirable on—

(1) Technique in methods of hybridization.
(2) The mode of inheritance of various characters.
(3) Hybrid vigor, including interspecies crosses.
(4) Factors affecting seed setting in alfalfa.
(5) Fundamental research on the nature and control of various diseases.

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(6) The mosaic problem.
(7) Effective means of isolating pure seed for increase.
(8) Interregional testing, including hardiness and disease tests.
(9) Production of improved seed.
(10) The use of the backcross method, or modifications, in alfalfa breeding.

INHERITANCE AND CYTOLOGICAL STUDIES

There is rather a large amount of literature dealing with the general genetic behavior of alfalfa, but very little has been done on the inheritance of any given character. This is to be expected in a crop worked with as little as alfalfa, but nevertheless it is a handicap to the plant breeder in many respects. As self-fertilized strains having a known inheritance are developed, more information of this kind should be forthcoming.

Most of the work so far has involved crosses between the two contrasting species, *Medicago sativa* × *M. falcata*. In such a cross Korohoda (*20*) has reported on the inheritance of flower color, shape of leaves, and structure of the stem. With regard to the inheritance of flower color in the purple × yellow cross, he states that the former supposition that two or three hereditary factors were involved was found to be inadequate. The results of his studies indicated at least four factors, one for each fundamental coloration—cream, blue, and violet—and one or two that intensify these colors.

With respect to the shape of the leaves of the hybrid, the shape typical of *Medicago sativa* was observed in the second generation in 28 plants, that typical of *M. falcata* in 196 plants, and an intermediate in 424 plants. It was not found possible to calculate the relations, assuming the existence of two, three, or four factors.

When examining the structure of the stem in the second generation, stems of the type of *M. falcata* were observed in 565 individuals, and of the type of *M. sativa* in 30 individuals. Since the ratio of these numbers (18:1) is close to 15:1, the workers assumed the existence of two hereditary factors, with the *falcata* type dominant over the *sativa* type.

MacVicar (*22*) reports the results of an investigation to determine the inheritance of black and white seed coat characters in alfalfa and whether or not the former could be utilized in breeding as a marker for identifying improved strains. He says:

> The available evidence indicated that the white seeded parent was homozygous for a recessive factor which results in the absence of yellow pigment, and that the inheritance of this character was comparatively simple. Inheritance of the black seeded character, on the other hand, was fairly complex, requiring the assumption of at least three factor pairs. The original black seeded plant was thought to have arisen as a single gene mutation. This gene, primarily responsible for pigmentation of the seed coat, together with at least two modifying factors was postulated as the most probable genetic factorial basis to account for the breeding behavior of the original black seeded parent.
>
> It was concluded that the character of black-seededness would be valueless from a utility standpoint.

The cytological aspects of alfalfa have also been neglected until recently, when several interesting papers have been published. Among these is a paper by Fryer (*12*), summarizing much of what is known regarding chromosome numbers in *Medicago* species, and another by Cooper (*6*) on embryology, reporting the important fact

that according to his observations the lack of seed production in various plants seems to be due not to lack of pollination or fertilization but to failure of the ovule to develop after it has been fertilized. In plants that fail to set seed after effective pollination takes place, the young embryos abort. Direct evidence regarding the cause of the abortion was not available, but it was believed to be an unbalanced nutritional condition.

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APPENDIX

INVESTIGATORS WORKING ON ALFALFA IMPROVEMENT

THE following list includes mainly the breeders and workers employed by institutions that returned questionnaires on superior germ plasm in alfalfa. Nearly all the workers listed as State agricultural experiment station employees devote only a small part of their time to alfalfa-breeding investigations. The remainder

of their time is given to investigations on other crops. This is also true of some of the field staff of the Division of Forage Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture. Early workers are listed on page 1233. The names of alfalfa breeders listed for foreign countries were all given in the returned questionnaires.

An asterisk (*) denotes United States Department of Agriculture employee.

United States

United States Department of Agriculture, Bureau of Plant Industry, Division of Forage Crops and Diseases, Washington, D. C.: H. L. Westover.*

California Agricultural Experiment Station, Davis: B. A. Madson, F. N. Briggs.

Colorado Agricultural Experiment Station, Fort Collins: D. W. Robertson, R. M. Weihing.

Kansas Agricultural Experiment Station, Manhattan: C. O. Grandfield.*

Kentucky Agricultural Experiment Station, Lexington: E. N. Fergus.

Michigan Agricultural Experiment Station, East Lansing: E. E. Down, S. T. Dexter, H. M. Brown.

Minnesota Agricultural Experiment Station, St. Paul: A. C. Arny.

Montana Agricultural Experiment Station, Havre: M. A. Bell.

Nebraska Agricultural Experiment Station, Lincoln: T. A. Kiesselbach, H. M. Tysdal.*

New Jersey Agricultural Experiment Station, New Brunswick: H. B. Sprague, E. M. Hodges.

New Mexico Agricultural Experiment Station, State College: J. C. Overpeck, G. N. Stroman.

New York Agricultural Experiment Station, Ithaca: C. H. Meyers.

Rhode Island Agricultural Experiment Station, Kingston: T. E. Odland, H. F. A. North.

Utah Agricultural Experiment Station, Logan: R. J. Evans, B. L. Richards, J. W. Carlson.*

Wisconsin Agricultural Experiment Station, Madison: R. A. Brink, A. H. Wright, O. S. Aamodt, E. J. Delwiche (Green Bay), A. L. Bibby (Spooner), A. M. Strommen (Spooner), L. E. Muskavitch (Ashland), F. R. Jones.*

Canada

Dominion of Canada Experimental Farms, Ottawa, Ontario. L. E. Kirk, J. M. Armstrong.

University of Saskatchewan, Saskatoon, Saskatchewan: T. M. Stevenson, William J. White.

University of Alberta, Edmonton, Alberta: J. R. Fryer.

Ontario Agricultural College, Guelph, Ontario: R. Keegan, O. McConkey.

McGill University, MacDonald College, Quebec: J. N. Bird.

Australia

Bathurst Experimental Farm, Bathurst: W. T. Atkinson.

Grafton Experimentl Farm, Grafton: W. H. Darragh.

Riverina Experimental Farm, Yanco: W. H. Poggendorff.

Hawkesbury Agricultural College, Richmond: N. S. Shirlow.

Wales

Welsh Plant Breeding Station, Aberystwyth: R. D. Williams.

Germany

Kaiser Wilhelm Institute, Munchberg: J. Hackbarth, Dr. Schrock.

Sweden

Sveriges Utsädesforening, Svalof: N. Sylven, O. Holmgren.

Sveriges Utsädesforening, Ultuna: R. Torssell.

TABLE 1.—*Historical summary of the development of improved varieties of alfalfa in the United States and Canada*

Variety or strain	Year introduced	Name and location of breeder	Superior characters	Breeding method used	Parent material	Present acreage: In State produced	Present acreage: Elsewhere
Grimm	1905	Wendelin Grimm, Minnesota.	Yield, quality, winter hardiness.	Natural followed by artificial selection.	Seed brought by Grimm from Germany.	700,000	(1)
Cossack	1907	N. E. Hansen, South Dakota.	Winter hardiness, productivity.	Selection from introduced strains.	Seed from Siberia		
Baltic	1908	Wheeler, South Dakota	Cold resistance, productivity	Natural selection	Probably Grimm, although not certain.	(1)	(1)
Grimm 19A	1909	do.	Winter hardiness, productivity.	Line selection	Grimm	100	
Ladak	1910	H. L. Westover, Samuel Garver, U. S. Department of Agriculture.	Yield, cold and drought resistance. More resistant to bacterial wilt than Grimm.	Selection of introduced material at Redfield, S. Dak.	Introduction from northern India as *Medicago falcata*.		
Ontario Variegated	1910	C. A. Zavitz and coworkers, Ontario.	Winter hardiness, productivity.	Inbreeding mass selections and strain building.	Variegated alfalfas from Baden and Alsace-Lorraine and various importations from Europe (Norway) and the original strain of Grimm.	500,000	7
Hardigan	1920	F. A. Spragg, E. E. Down, Michigan.	Yield of hay and seed	Selection	Baltic	400,000	5,000
Meeker Baltic	1920	P. K. Blinn, Colorado	Yield, cold resistance, hay quality.	Natural selection and selection.	do.	20,000	
Grimm 451	1921	J. Bracken, L. E. Kirk, Saskatchewan.	Hardiness, yield	Mass selection	Several Grimm introductions, all tracing back to Minnesota Grimm.	4,000	
Grimm 666	1925	M. Champlin, L. E. Kirk, Saskatchewan.	Seed yield	Single plant line	Selection from Grimm obtained from Lyman of Excelsior, Minn.	1,000	
Hardistan	1930	A. Hecht, T. A. Kiesselbach, A. Anderson, G. L. Peltier, Nebraska.	Bacterial wilt resistance	Selection	Old Nebraska field, probably of Turkistan origin.	375	25
Grimm, M. C.	1931	J. N. Bird, Quebec	Winter hardiness	Recombination selfed lines and strain.	Grimm stock 8, Grimm stock 5, obtained from University of Minnesota in 1911, S. P. I. 29988.	[2] 25	
Kaw	1932	S. C. Salmon, C. O. Grandfield, Kansas.	Resistance to wilt and cold	Natural selection	Provence 34886	(3)	
Kansas 308	1933	C. O. Grandfield, Kansas.	Resistance to wilt and cold, high yield.	do.		15	
S133	1935	R. D. Williams, Wales.	Under test. Increased yields on comparatively poor soils.	Built up from 10 selfed lines.	Mainly Grimm and Canadian Variegated.	(3)	
A number of strains	1920-36	F. A. Spragg, E. E. Down, S. T. Dexter, H. M. Brown, Michigan.	Superior seed production, yield, and cold resistance.	Hybridization selection	Hardigan	(4)	

Approximately 50 strains.	1928–36	H. M. Tysdal, G. L. Peltier, T. A. Kiesselbach, Nebraska.	Wilt and cold resistance, seed production.	Selection in self-fertilized lines, hybridization and selection in F_2.	Plants from old Nebraska fields, introductions from foreign countries, domestic varieties including Cossack, Ladak, *Medicago* sp.	(4)	--------
Unnamed----------- --	(1)	J. R. Fryer, Alberta. --	Accumulation of hereditary factors that contribute to fertility.	Maternal line selection--- --	Grimm, Wiley, Grimm, Disco, Southworth's hybrid, and Ontario Variegated.	(3)	--------
A number of strains---	1930–36	R. A. Brink, F. R. Jones, H. R. Albrecht, Wisconsin.	Wilt and cold resistance, seed production.	Selection in self-fertilized lines, hybridization.	Grimm, Cossack, Ladak, Turkistan, Kansas and Montana Common, introductions.	(4)	--------
Do---------------	1932–36	H. B. Sprague, Glenn Burton, New Jersey.	Adaptation for New Jersey conditions.	Mass selection, hybridization--	Peruvian, *Medicago falcata*, selected lines from other States.	(4)	--------
Do---------------	1930–36	C. O. Grandfield, Kansas	Wilt resistance, Kansas Common type.	Selection in self-fertilized lines, hybridization.	Kansas Common, Kaw, Turkistan, introductions.	(4)	--------
Do---------------	1934–36	G. C. Moe, C. H. Myers, D. B. Johnstone-Wallace, New York.	Pasture types, seed setting -	Hybridization, selection -	Grimm, *Medicago falcata*------	(4)	--------

[1] Unknown.
[2] In Province of Quebec.
[3] Not yet distributed
[4] Not yet released.
[5] Now in process.

Key to Some of the Commoner Species of Medicago

		Chromosome number (2n)
Pods not coiled, straight or curved; flowers yellow.		
Pods not flattened.		
Pods kidney-shaped, one seeded, style as long as ovary at time of blooming	M. LUPULINA	16
Pods straight or curved, several seeded, usually sickle-shaped, style never as long as ovary.	M. FALCATA	[1] 32
Pods flattened, at least twice as broad as in *M. falcata*.		
Pods large, oval, many seeded	M. PLATYCARPA (M. PLATYCARPOS).	16
Pods smaller, with about four seeds	M. RUTHENICA	16
Pods spirally coiled.		
Coil with an open center; plants perennial.		
Shrubby, 4 to 10 feet high; flowers large, yellow.	M. ARBOREA	32
Herbaceous plants; flowers usually not yellow.		
Pods but little coiled, less than a full spiral.	M. HEMICYCLA	32
Pods with one to several windings.		
Flowers uniformly violet or blue	M. SATIVA	32
Flowers variegated, white, yellow, and blue.		
Plants generally without rhizomes.		
Plants glabrous or slightly pubescent.	M. MEDIA	32
Plants glandular pubescent, especially pods and calyx and young shoots.	M. GLUTINOSA	32
Plants with long rhizomes; flowers, seeds, and pods larger than in *M. media*, pod with two and a half to four windings.	M. GAETULA	32
Coil with a closed center; flowers yellow; annuals.		
Pods generally spiny.		
Spines in a double row, those at top of bur turned upward to form a double crown.	M. CORONATA	16
Spines not as above.		
Leaves with a dark blotch in center; seed with a projection by the hilum.	M. ARABICA	16
Leaves without a dark blotch.		
Pods 7 to 10 mm across spines from half to whole width of winding.	M. HISPIDA	14
Pods as above, but spines shorter	M. HISPIDA DENTICULATA	14
Pods without spines.		
Pods small, about size of those of *M. hispida*.	M. HISPIDA CONFINIS	14
Pods much larger.		
Pods flattened; leaflet nearly orbicular	M. ORBICULARIS	16
Pods nearly spherical; leaflets nearly twice as long as wide.	M. SCUTELLATA	32

[1] Also 16

Brief Description of Certain Medicago Species With Particular Reference to Their Economic Desirability

Medicago platycarpa is a low-growing perennial with large broad leaflets, yellow flowers, and large flat pods, found mainly in Siberia. According to Hansen its distribution is mainly along the edges of timberland and in open places in the native

timber, indicating that it might be adapted to sheltered regions such as the timber sections of northern Minnesota and Wisconsin and westward into the Rocky Mountains.

M. ruthenica is a small semierect perennial with small narrow leaflets, yellow flowers, and small pods. Hansen found this species growing wild in a section of the Gobi Desert in nearly pure sand. In general it is found scattered in dry, stony soils. As a fodder plant this species is greatly relished by the cattle, horses, sheep, and camels kept by the Mongolian nomads. Its distribution is farther north than that of Common alfalfa (*M. sativa*).

M. arborea is the largest representative of the *Medicago* genus, attaining a height of upward of 10 feet. It is a native of the Mediterranean region of Europe and does not thrive in cold climates. It is cultivated to a limited extent in various portions of its range, but as it gets woody too quickly and is less productive than *M. sativa*, that species is much more in favor.

M. falcata is an upright to prostrate perennial with small elongated leaflets, yellow flowers, and falcate pods. It is distributed over a wide range in eastern Europe and western Asia. Apparently it combines readily with *M. sativa* to form many of the cultivated varieties such as Grimm and Cossack, which are classified as *M. media* in the foregoing key. Many strains, though not all, are very cold-resistant, and certain types also endure pasturing rather well. It is now being used in breeding programs to a considerable extent.

A point of particular interest has recently been raised by Fryer (*12*), who found different chromosome numbers in *M. falcata*. In two strains he found the number to be $2n = 32$, while in another strain he found it to be $2n = 16$. It is probable these two types would react differently in crosses.

M. gaetula is particularly noted for its rhizomes, by means of which it spreads readily like sod-forming grasses. It is now being used in crosses to produce pasture and soil-binding types.

M. glutinosa is a native of the Caucasus Mountains and Trans-Caucasia generally, especially of Armenia, where it is found up to an elevation of 7,500 feet. It is found growing in a very dry upland region and is more vigorous than most *Medicago* species of Caucasia.

M. hemicycla is found in the Caucasian region and is somewhat similar in morphological type to *M. media*. It is considered to be a natural cross between *M. sativa* and *M. falcata*.

M. coronata is remarkable on account of its very high drought resistance. It is an annual found in all parts of Palestine, but its occurrence on the mountain slopes is particularly interesting, as the soil there is only an inch or two deep over the rocks. The seed setting of this variety is also high.

McKee and Ricker (*21*) state that the nonperennial species of *Medicago* consist principally of bur-clovers, mostly annual plants native to the Mediterranean region. Spotted bur-clover (*M. arabica*), California bur-clover (*M. hispida*), and black medic (*M. lupulina*) are the only species now widely distributed in the United States. The feeding value of bur-clovers, both those with and those without spines, is good. Among the latter the three most promising are *M. confinis*, *M. orbicularis*, and *M. arabica inermis*.

IMPROVEMENT IN SOYBEANS

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ONE of the most striking agricultural developments of recent times is the rapid rise of the soybean within the last few years from the position of a substitute and emergency crop to a place of considerable economic importance in American agriculture and industry. First introduced into this country in 1804, it was grown for many years only in gardens as a curious plant from the Far East. Its culture has now spread over much of the territory east of the Mississippi River, and it has become well established in the cropping systems of this area as well as in the States bordering the west bank of the Mississippi.

The high nutritive value of the plant and its seeds has made it particularly valuable as a livestock feed. The seed, with its by-products, oil and oil meal, have great commercial possibilities as a food and for industrial purposes. In spite of the extensive investigations that have been conducted, the work of developing this versatile plant to its fullest possibilities is still in its infancy. While much has been done in determining the genetic relations of many seed and plant characters, the plant breeder has many problems of a complex nature ahead in the development of new and better varieties for the various purposes for which the crop is now being used.

HISTORY OF THE SOYBEAN

THE early history of the soybean is lost in obscurity. Ancient Chinese literature, however, reveals that it was extensively cultivated and highly valued as a food centuries before written records were kept. It was one of the grains planted by Hou Tsi, a god of agriculture. The first record of the plant is contained in a materia medica describing the plants of China, written by Emperor Sheng Nung in 2838 B. C. The crop is repeatedly mentioned in later records, and it was considered the most important cultivated legume and one of the five sacred grains essential to the existence of Chinese civilization. Seed of the plant was sown yearly with great ceremony by the Emperors of China, and poets extolled its virtues. The records of methods of culture, varieties for different purposes, and numerous uses indicate that the soybean was perhaps one of the oldest crops grown by man.

Botanically the soybean usually has been referred to in literature as *Glycine hispida* (Moench) Maxim. In an extensive botanical

[1] The authors are greatly indebted to C. M. Woodworth and L. F. Williams, of the Illinois Agricultural Experiment Station, for their cooperation and suggestions in the preparation of this article.

study Piper (fig. 1) came to the conclusion that the soybean must be named *Soja max* (L.) Piper. Other botanists, however, consider *Glycine javanica* L. the type species of *Glycine* and call the soybean *Glycine max* (L.) Merrill.

The cultivated soybean is thought by many investigators to have been derived from *Glycine ussuriensis* Regel and Maack, which grows wild throughout much of eastern Asia. This species is prostrate in habit of growth, has long fine twining stems, small narrow leaves, appressed hairs, purple flowers, small compressed pods, and small oblong seeds of a sooty-black color. Karasawa (*9*)[2], on the basis of genetic data, believes the cultivated soybean might have been derived from this wild species through the qualitative and quantitative changes due to gene mutation, unaccompanied by any change in chromosomes. A plant with characters between the wild and the cultivated species has been described by Skvortzov (*33*) as *G. gracilis* Skvortzov.

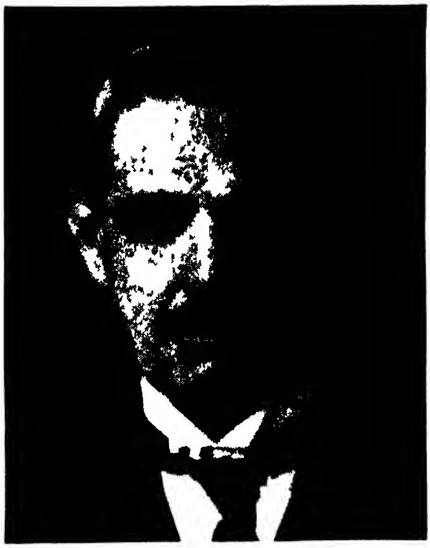

Figure 1.—The late Charles Vancouver Piper, agronomist, United States Department of Agriculture, 1902–26. Pioneer in the introduction and development of soybean varieties for United States conditions.

Europeans knew of soybeans in the seventeenth century, and they were tried in Germany, England, France, and Hungary but did not become commercially established in any part of Europe until in recent years.

The first mention of the soybean in American literature was in 1804, when James Mease wrote: "The soybean is adapted to Pennsylvania and should be cultivated." In 1889 W. P. Brooks, of the Massachusetts Agricultural Experiment Station, brought a number of varieties from Japan, and in 1890 C. C. Georgeson, of the Kansas station, secured three lots from the same country. Undoubtedly other early importations of seed from Asia were obtained through missionaries, but no definite records have been found. Since 1890 most of our agricultural experiment stations have experimented with soybeans and many bulletins have been published dealing wholly or partly with the crop.

In 1898 the Department started to introduce large numbers of soybeans. Previous to this there were not more than eight varieties, with limited adaptation to soil and climate, grown in the United States.[3] Since that time the acreage of soybeans in the United States has in-

[2] Italic numbers in parentheses refer to Selected References on the Genetics of the Soybean, p. 1181.
[3] The eight varieties of soybeans grown in the United States were Ito San, Mammoth Yellow, Butterball, Buckshot, Kingston, Guelph or Medium Green, Eda, and Ogemaw.

creased more than a hundredfold—from less than 50,000 acres in 1907 to nearly 5,500,000 acres in 1935. The increase in acreage and production in this country has been closely correlated with the introduction of varieties from the Orient and their development through selection.

WORLD DISTRIBUTION AND PRODUCTION

The soybean is grown to a greater extent in Manchuria, often called "The Land of Beans", than in any other country in the world (fig. 2). It occupies about 25 percent of the total cultivated area and is the cash crop of the Manchurian farmer (fig. 3). Chosen and Japan are large producers, and south of China the soybean is cultivated more or less in the Philippines, Siam, Cochin China, India, and the East Indies.

In the central part of the Union of Soviet Socialist Republics the districts of the Don and the southwest are said to be especially suited to the culture of this crop. In Czechoslovakia, in 1935, commercial beans were produced on a small scale. Rumania has also succeeded in growing soybeans of high quality, and the production of seed is rapidly increasing. In other parts of the world, particularly Germany, England, South Africa, British East Africa, Algeria, Egypt, New South Wales, and New Zealand, soybeans have been tried or are being grown in a small way.

In the Western Hemisphere the production of soybeans is concentrated chiefly in the Corn Belt region of the United States. In 1920,

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ONE *of the most striking agricultural developments in the United States in recent times is the rapid rise of the soybean. In 1907 there were 50,000 acres; in 1935, nearly 5,500,000. In 1920, seed production was 3,000,000 bushels; in 1935, about 40,000,000. Remarkable progress has been made in the last few years in developing food and industrial uses. Soybean breeding to meet varied cultural, food, and industrial needs is being conducted by the United States Department of Agriculture and by experiment stations in 32 States, and more than 10,000 introductions have been made for study and experiment. In spite of extensive investigations, the work of developing this versatile plant to its fullest possibilities is still in its infancy. But though the plant breeder has many problems of a complex nature ahead, there appears to be no reason why it should not be possible, by selection and hybridization, to develop varieties that possess all, or nearly all, the important characters desired by oil processors and by manufacturers of food and industrial products.*

14 States produced 3,000,000 bushels of seed, the leading States being North Carolina, Virginia, Alabama, Missouri, and Kentucky—North Carolina producing about 55 percent of the total. By 1931, seed production had increased to nearly 15,500,000 bushels, with Illinois, Indiana, North Carolina, and Missouri leading. In 1935, about 40,000,000 bushels of seed were produced, of which about 37,500,000 bushels (92 percent) were harvested in Illinois, Indiana, Iowa, Missouri, and Ohio, the first three States producing about 87 percent of the total. In Canada, production is confined chiefly to the Province

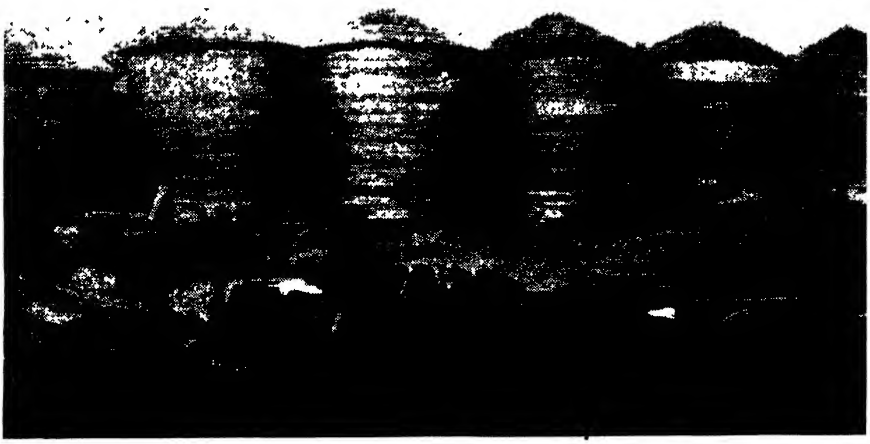

Figure 2.—Storage yard of a Chinese grain merchant near Kungchuling, Manchuria. More than 80 osier bins, each holding four carloads of soybeans, were in this yard.

of Ontario, where about 15,000 acres are planted to this crop. In other parts of the Western Hemisphere the acreage grown in any country is small.

Table 1 shows the increase in production of soybeans over an 11-year period, 1924–25 to 1935–36 inclusive, in the principal producing countries of the world.

TABLE 1.—*Increase in production of soybeans over an 11-year period, 1924–25 to 1935–36, inclusive, in the principal producing countries of the world* [1]

Country	Production in— 1924–25	Production in— 1935–36
	Bushels	*Bushels*
Manchuria	92, 667, 000	140, 444, 000
Chosen	18, 723, 000	[2] 21, 961, 000
Japan	15, 367, 000	[3] 13, 307, 000
United States	5, 190, 000	39, 637, 000
Netherland India	3, 536, 000	[2] 6, 676, 000

[1] From the following publication: U. S. Dept. Agr., Agricultural Statistics 1936.
[2] 1934–35. [3] 1933–34 (decrease).

Figure 3.—The Manchurian farmer still harvests (*A*), threshes (*B*), and cleans (*C*) soybeans by hand methods inherited from his ancestors, whereas in the United States (*D*) modern machine methods are used.

UTILIZATION OF THE SOYBEAN

In the Orient the soybean is grown principally for the seed, which for centuries has been utilized in the preparation of a great variety of fresh, fermented, and dried food products indispensable in the diet of oriental people. Large quantities of beans are also crushed for oil, which is used for food and numerous industrial purposes; and the resulting cake or meal (fig. 4) is utilized chiefly as a fertilizer and to a small extent as feed for animals. European oil mills have for many years imported considerable quantities of soybeans from Manchuria (fig. 5) for crushing for oil and oil meal.

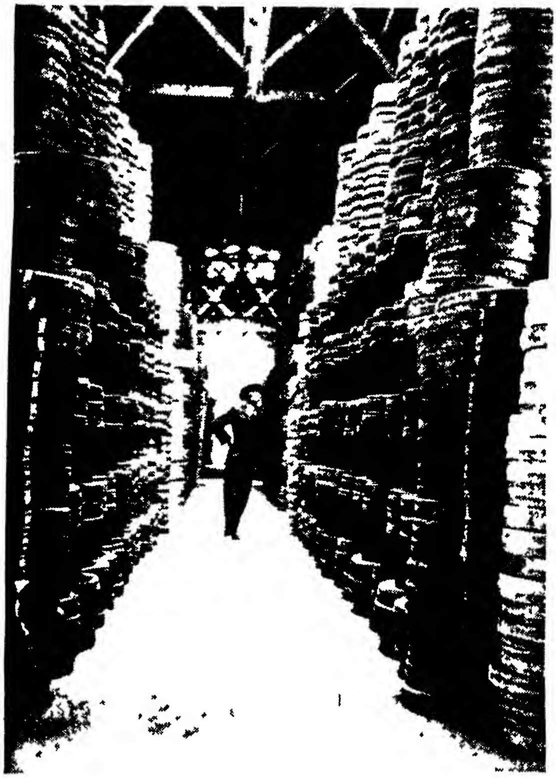

Figure 4.—Millions of soybean oil cakes are stored in warehouses in Manchuria awaiting shipment to Japan, Chosen, China, and the East Indies, where they are used for fertilizing purposes and for cattle feed.

The soybean is used in the United States primarily for forage purposes, being either preserved as hay or silage or cut and fed green as soilage. It is also pastured extensively with hogs and sheep, and is used to some extent as a green manure or cover crop For many years the increasing supply of seed was matched by a steady demand for planting the expanding acreage and for use as a stock feed, but eventually other outlets had to be found. About 1920 the possibilities in home-grown soybeans attracted the attention of oil mills, and by 1929 they began to be a potent factor in the production of the crop for commercial purposes. In 1926 slightly more than 2,500,000 pounds of oil were produced in the United States, while more than 200,000,000 pounds were obtained from the 1935 crop.

Remarkable progress has been made in the last few years in developing food and industrial uses for the soybean, the oil, and meal. At present about 45 oil mills, including a few cottonseed oil mills, are crushing soybeans; more than 40 concerns are manufacturing soybean food products and soybean flour; and more than 75 factories are

turning out various industrial products made from soybeans. Soybean oil has become an important product in many industries. In addition to the use of the meal in livestock feeds, considerable quantities are utilized in the manufacture of foods and industrial products. The high nutritional value of the soybean, known for many centuries in oriental countries, is becoming quite generally recognized in the United States. Many food concerns in various parts of the country are manufacturing numerous products wholly or in part from the soybean.

The following outline shows the diversity of uses to which the different products of the soybean are put:

SOYBEAN UTILIZATION

- Soybean
  - Plant
    - Forage. Green manure. Pasture.
      - Fuel.
      - Furfural.
      - Hay.
      - Silage.
      - Soilage.
  - Bean
    - Meal
      - Celluloid substitutes.
      - Core binder.
      - Feeds
        - Cattle.
        - Dogs
        - Fish.
        - Hogs.
        - Poultry.
        - Rabbits.
        - Sheep.
      - Fertilizer.
      - Glue.
      - Human food
        - Beer brewing.
        - Flour. (See Dried bean.)
        - Seasoning powders.
        - Soy sauce.
        - Vegetable milk.
      - Plastics.
      - Water paints.
    - Oil
      - Candles.
      - Celluloid.
      - Core oil.
      - Disinfectant.
      - Electrical insulation.
      - Enamels.
      - Food products
        - Butter substitutes.
        - Cooking oils.
        - Lard substitutes.
        - Salad oils.
        - Medicinal oil.
      - Fuel.
      - Glycerin.
      - Insecticides.
      - Lecithin
        - Candies.
        - Chocolate.
        - Cocoa.
        - Emulsifier.
        - Margarine.
        - Medicines.
        - Textile dyeing.
      - Lighting.
      - Linoleum.
      - Lubricant.
      - Oilcloth.
      - Paints.
      - Printing ink.
      - Rubber substitutes.
      - Soaps
        - Hard.
        - Liquid.
        - Soft.
      - Varnishes.
      - Waterproof for cement.
      - Waterproof goods.
    - Green bean
      - Canned.
      - Frosted.
      - Green vegetable.
      - Salad.
    - Dried bean
      - Baked.
      - Boiled.
      - Breakfast foods.
      - Feeds
        - Cattle.
        - Hogs.
        - Poultry.
        - Sheep.
      - Flour
        - Baked products.
        - Breakfast foods.
        - Candies.
        - Chocolate.
        - Diabetic foods.
        - Health drinks.
        - Ice-cream cones.
        - Ice-cream powder.
        - Infant foods.
        - Macaroni products.
        - Meat products, filler.
      - Roasted
        - Candied.
        - Coffee substitute.
        - Salted.
      - Soy sauce.
      - Sprouts.
      - Vegetable milk
        - Casein
          - Paints.
          - Paper size.
          - Textile dressing.
          - Waterproofing.
        - Condensed.
        - Curd
          - Canned.
          - Dried.
          - Fermented.
          - Fresh.
          - Smoked.
        - Foods.
        - Powder.

Figure 5.—Coolies loading soybeans on a freighter for shipment to the oil mills of Europe.

IMPROVEMENT OF SOYBEAN VARIETIES

Soybean breeding is being conducted in the United States, Japan, Manchuria, China, India, Chosen, and the Union of Soviet Socialist Republics, and to some extent in a few European countries. As with other crops, the chief objective has been increased yield under local conditions. Within the last few years, however, with increased utilization of the soybean for industrial and food purposes, attention has also been given by plant breeders to the oil and protein content, the nutritive value, and the quality of beans.

In the United States, more than 50 percent of the acreage devoted to soybeans is used for forage and pasture; breeding work, therefore, has tended largely toward the development of varieties for hay, silage, and pasture. The development of such varieties as Virginia, Laredo, Otootan, Wisconsin Black, Manchu, Wilson-Five, Kingwa, Peking, and Ebony by selection from introductions has been the principal factor in the increased use and acreage.

Beginning with 1929, the use of soybean seed by oil mills has led to a demand for yellow-seeded varieties of high oil content. Agronomists and plant breeders have attempted to meet this demand by making large numbers of selections from foreign introductions and locally grown varieties and by analyzing these for oil content. This has brought about the development of several superior oil varieties and has resulted in a large increase in production of beans for milling purposes. The most popular of these varieties are Illini, Dunfield, Mukden, Mandell, Scioto, Mansoy, Manchu, Mamredo, Delsta, and Mandarin. Results of analyses with more than 1,000 selections and varieties have shown a range of from 12 to 26 percent in oil content. From studies of the oil content of varieties grown in a given locality,

it seems possible, from the breeding standpoint, to produce varieties high or low in oil, at least within the known ranges of variation exhibited by common varieties.[4]

Quality, which may include several characters, the most important of which are the iodine number and the lecithin value, is the chief factor in the use of soybean oil. The drying property of an oil is

Figure 6.—Prize winners. Manchurian farmers are awarded certificates and prizes for producing high-quality soybeans.

measured by the iodine number, that of linseed being about 180. In a large number of tests with varieties and selections of soybeans, the iodine number ranged from 118 to 141. The iodine number of the wild soybean was found to be 155. To give soybean oil a better drying quality for paint purposes, its number must be raised. On the other hand, it is stated that oil with a low iodine number is more suitable for food purposes. Lecithin, a phosphatic compound, of which egg yolk was the chief source of supply, is now being extracted from soybean oil on a commercial scale. It is used extensively in the baking and confectionery trades, and also in textile and leather industries. Varietal studies show a range of 1½ to 3 percent, according to variety. The development of varieties high in lecithin and high and low in iodine number offers a most promising problem to the plant breeder. The best procedure in breeding for quantity and quality

[4] The Agricultural Experiment Station of the South Manchuria Railway at Kungchuling, Manchuria, has conducted experiments for several years toward the selection of varieties for high oil content. One variety, the Kungchuling, with seed uniform in size and shape and an oil content of more than 20 percent, has been widely distributed. To encourage the growing of this variety in regions to which it has been found adapted, the Experiment Station holds an annual soybean fair at which prizes are given to the farmers having the highest quality of seed (fig. 6).

of oil in the soybean is without doubt to analyze adapted varieties and then to isolate the best line from the best variety.

The development of new industrial uses for protein from the soybean and the value of this constituent in foods and feeds has led investigators to give more attention to varietal differences in the amount and quality of protein. Extensive analytical tests show a range of from 28 to 56 percent of protein (moisture-free basis), depending on variety and locality. Investigations of the nutritive value of soybean protein have shown that it contains all the essential amino acids. Studies by the Bureau of Chemistry and Soils of the United States Department of Agriculture with several standard varieties show a wide range in percentage of three amino acids—cystine, tryptophane, and tyrosine—which indicates the possibility of developing varieties of high nutritive value for animal feeds and human foods.

In the Orient, soybean foods to a very considerable extent supply the protein that is furnished largely by meats in the diet of western people. Oriental varieties of soybeans are distinguished not only according to seed and plant characters but also according to use, as for bean curd, bean sprouts, confections, and other food products. Increased recognition of the nutritional value of the soybean in the United States has created a demand for varieties more suitable for this purpose, since the varieties generally grown for commercial uses are not desirable for food. The principal drawbacks to the use of dried beans have been the length of time necessary for cooking and the flavor. Experiments with a large number of selections and varieties used in the Orient showed considerable variation. Some were of excellent flavor and became soft in less than 2 hours of cooking, while others remained hard and had little flavor or a pronounced bean flavor. Several of the most promising have been tested in various sections and the Easycook, Bansei, Rokusun, Jogun, Chusei, and Sousei are now in the hands of growers and seedsmen. Experiments by commercial firms have shown that these varieties are superior to commercial varieties for the manufacture of food products, such as bean flour, roasted beans, bean milk, and bean curd.

In Japan, certain varieties of soybeans were found that were used solely as green shelled beans. Ranging in maturity from 75 to 170 days, many of these introductions, and selections from them, have been found especially promising for various sections in the United States. The vegetable soybean offers an excellent food of high nutritional value, especially in the fall when other green beans are lacking and in sections where the Mexican bean beetle prohibits the growing of garden beans. As a result of selection, cooking tests, and adaptation studies, eight green vegetable varieties—Hahto, Kura, Kanro, Hokkaido, Higan, Chusei, Sousei, and Jogun—have been introduced in various sections of the country.

Although the major objective of soybean breeding has been to increase acreage yields, increasing utilization for food and industrial purposes demands improvement in quality as well as yield. With the vast number of introductions now under test by the Department and State experiment stations, there appears to be no reason why it should not be possible, by selection and hybridization, to develop varieties that possess all, or nearly all, the important characters desired by oil processors and by manufacturers of food and industrial products.

ADAPTATION

The soybean seems to be peculiarly sensitive to changes of soil and climate. Differences in behavior of the same pure-line variety in different localities are often very striking, so much so that it is often difficult to believe the variety is the same. Obviously, this adaptation explains why practically every locality in the soybean regions of the Orient has its own local varieties. Of the many varieties introduced into the United States, the same variety has rarely been secured a second time unless it was obtained from the same locality. In the Orient, limited areas appear to have varieties adapted to their own soil and climatic conditions. For the most part, Japanese varieties are unsuited to Manchuria and Chosen (Korea), and on the other hand, few Manchurian and Korean varieties are suited to Japan. Very few Korean varieties are adapted to the soil and climate of Manchuria. In these countries centuries of experience, aided by natural crossing and natural selection, have brought about the development of varieties adapted to special purposes. In China, Japan, Manchuria, and Chosen varieties are found especially suited for bean curd, bean milk, bean sprouts, green vegetable beans, bean flour, bean confections, oil and oil meal, and fermented products. Different regions in these countries have their own different varieties for these purposes

One of the outstanding results of soybean improvement work in the United States has been the realization of the importance of varietal adaptation. Early investigators noted that introductions from various localities in the Orient differed widely in their adaptation to various regions or localities in this country. This led to the conclusion that by introduction and local selection strains adapted to all localities, conditions, and purposes could be developed. With the increase in the number of introductions and the development of new varieties from these for a greater range of soil and climatic conditions, the acreage in commercial plantings has increased.

In many regions of the United States adaptation experiments comparing standard varieties with newly developed sorts or new introductions indicate that the new types are better adapted than the commonly grown varieties, and it seems likely that varieties for different uses that suit requirements in nearly all our farming regions will be found. At present about 100 named varieties (see appendix, table 4) are generally grown or are being increased for greater distribution in this country. Although it would be highly desirable to limit the number of varieties in the trade, unfortunately each region must have locally adapted varieties suitable for different purposes in order to obtain the best results.

METHODS IN BREEDING

The soybean is normally a self-fertilized plant, the flowers being perfect, producing both pollen grains and ovules. The flowers are completely self-fertile, as shown by experiments carried on by Piper and Morse (*30*) at the Arlington Experiment Farm, Arlington, Va. (near Washington, D. C.), in 1909. Screened or bagged plants set pods and seeds as perfectly as plants in the open. Similar experiments by Woodhouse and Taylor (*54*) in India gave identical results. As

pollination occurs about as soon as the flower opens or a little before, there is little opportunity for cross-pollination to take place. However, natural crossing does occur. Since the plant is self-fertilized, the same general principles of breeding that apply to other self-fertilized crops may be applied to the improvement of the soybean.

Selection within self-fertilized plants is effective in purifying existing strains and makes some improvement possible, but variations are essential for any great improvement within a crop, and the only practical means the plant breeder has of inducing variations is by hybridization. By this method he may combine desirable characters from different varieties in one type and obtain plants that express a character to a greater or lesser extent than it was expressed in either parent. As with other crops, the major problem in the improvement of the soybean is to bring together into one type all the characters that are considered desirable for a certain set of conditions. From this standpoint, hybridization holds much promise for the development of special varieties of soybeans. This involves close study of wild and domestic species, varieties, and strains and their reactions to environment, as well as quantitative and qualitative analysis of oil, protein, and other constituents of the seed.

After varieties are selected or developed the grower faces the problem of maintaining them as pure strains. Commercial varieties of soybeans are in general relatively pure because the plant is self-fertilized. However, in a field of a single variety one often finds more or less offtype plants. Such mixtures may be brought about by careless methods of planting and threshing, by natural crossing, and by mutation. No natural crossing will result if mechanical mixtures are avoided. Mutations rarely occur and therefore are not an important factor. A variety can be kept relatively pure by careful methods of planting and threshing and by roguing out offtype plants.

Natural and Artificial Crossing

Previous to 1907 it was quite generally assumed that natural crossing in the soybean did not occur. In that year oddly colored seeds were noted in the variety rows and plots at the Arlington Experiment Farm, and were selected by Piper and Morse (*30*). The progeny of these seeds in 1908 showed segregation for various seed and plant characters. In that year more than 100 single plants of supposed hybrid origin were selected and most of these broke up in the following year in simple Mendelian proportions, indicating that they were natural hybrids. It is often easy to detect hybrids by the peculiar coloration of the seeds (fig. 7). Among the more striking colors are yellow or green with narrow streaks or bands of black or brown beginning usually at the hilum and extending over half or more of the seed, or mainly centered about the hilum. Hybrid plants are also often distinguished by the unusual form of the pods near the tips of the branches. They are more swollen and the seeds are more crowded than normal; the pods are often thinner walled and much less pubescent, sometimes being nearly smooth.

Natural crossing in soybeans has been studied to some extent by various investigators and it is quite generally agreed that a limited amount does occur, but that it is much less than 1 percent.

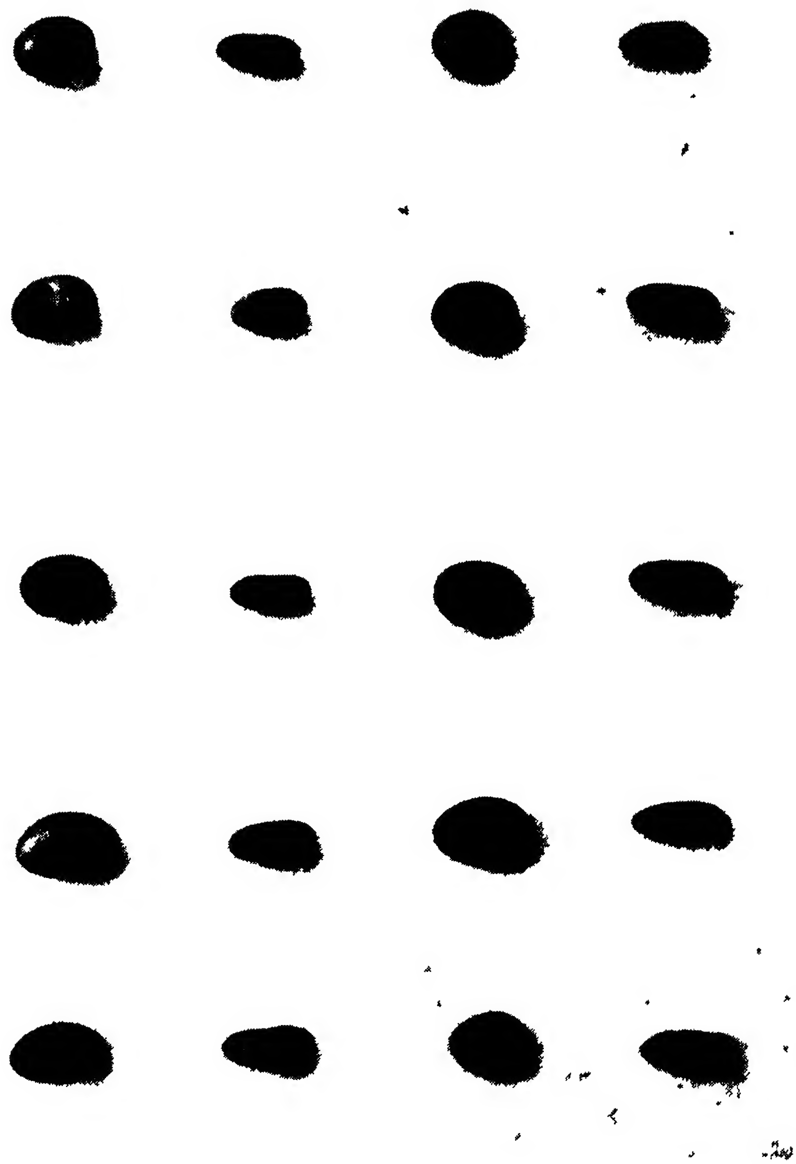

Figure 7.—Seeds of a natural soybean hybrid showing peculiar types of coloration.

Even this small amount of natural crossing undoubtedly is responsible for many of the mixtures now occurring in our standard varieties. The crossing is made possible by the mechanical mixing of seed through careless methods of planting and harvesting. After finishing with one variety, the planters or harvesters are not thoroughly cleaned before starting on another, so that the two varieties are mixed in the same field. An excellent illustration of this is afforded by the Mammoth Yellow variety now produced in eastern North Carolina. For many years this was the only variety grown in that section and it remained pure. As other varieties were introduced, the Mammoth Yellow seed became more or less mixed and it is now difficult to find fields without offtypes.

Natural crossing in soybeans is undoubtedly brought about by small insects. Thrips have been observed to be very common in the soybean flowers at the Arlington Experiment Farm. Bees and other insects have also been observed working on soybean flowers. Studies by many investigators at various places indicate that soybean plants growing in contact with one another are more likely to be crossed than plants separated by a few feet.

Because the flower is very small and easily injured, the work of making artificial crosses with the soybean is a difficult and tedious operation. Under field conditions at the Arlington Experiment Farm, Piper and Morse (*31*) made successful crosses in about 20 percent of the operations. In the greenhouse, where it is difficult to secure normal behavior in the soybean plant in winter, no success has thus far attended efforts to produce hybrids. Under winter conditions, the plants are small and bear few flowers, which do not develop and open normally and which apparently become fertilized in the very early bud stage. Woodworth (*63*), in crossing studies, found that soybean crosses can be made in the greenhouse as well as in the field provided artificial light is used. Light from 500-watt bulbs was used in the early stages of plant growth to induce good vegetative development, and then the light was shut off to induce flowering. The percentage of successful crosses is said to compare favorably with that ordinarily obtained under field conditions.

Crossing the flowers in the afternoon from 3 to 7 o'clock has given the best results, and it also has been found best to emasculate and pollinate a flower the same afternoon. Experience has shown that emasculation is the most difficult part of the operation and must be performed before the soybean flower has fully opened. All of the flower buds should be removed from the raceme except those to be crossed, and in these the purple or white of the corolla must have appeared above the calyx. At this stage, the 10 anthers surrounding the stigma (fig. 8) are immature and may easily be removed without bursting the pollen sacs. After emasculation, pollination is a relatively simple process, the pollen being applied to the stigma at once. In collecting the pollen for crossing, it is advisable to select well-developed flowers just before they open or fresh-looking flowers that have just opened. After the pollen has been applied, the raceme should be enclosed in a small paper or cloth bag, or a leaf may be pinned around it to protect the parts from excessive evaporation.

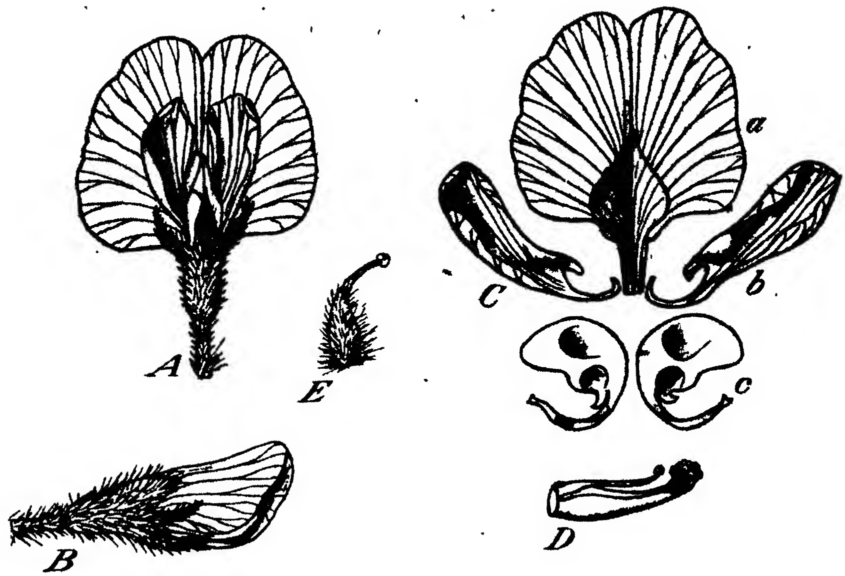

Figure 8.—Soybean flower and parts enlarged: *A*, Front view; *B*, side view; *C*, parts of the corolla (*a*, standard; *b*, wing; *c*, one of the keel petals); *D*, stamens; *E*, pistil.

Mutations

The origin of new varieties of soybeans without hybridization has apparently occurred in several instances that have come under the observation of investigators. Piper and Morse (*30*) cite a case in which a brown-seeded type, the Trenton, arose as a mutation from a yellow-seeded variety, the Mammoth Yellow. Grown side by side at the Arlington Experiment Farm, these varieties were indistinguishable by any character other than the seed color. Woodworth (*63*) explains this by assuming that the gene designated as *ii*, carried by the Mammoth Yellow variety, mutated to the gene designated as *i*, and that this permitted the brown pigment of the Mammoth Yellow hilum to extend over the whole seed coat to produce a brown bean.

A more recent mutation gave rise to the Avoyelles variety. This variety with medium-sized black seed was selected in Louisiana from a field of Otootan, a small black-seeded type, and it gave uniform progeny that in many characters is superior to Otootan. Stewart and Wentz (*36*) discovered a recessive glabrous type which they designated by the symbol p_2 and assumed that it arose as a mutation. Woodworth (*63*) notes the following mutations that have come under his observation: Dark to light pod, normal plant size to dwarf, normal green plant to variegated, and black hilum to brown hilum. In addition to these he has noted a few mutations in vegetative cells that resulted in "chimeras" of various kinds.

Hybrid Vigor

The phenomenon of heterosis, or hybrid vigor, in soybeans was first reported by Wentz and Stewart (*50*), who found in the first-generation hybrid of some crosses considerable increases in height of plant over the average of the parents. Still greater evidences of hybrid vigor were shown by the hybrids in yield of seed, the percentage increases over the parents ranging from 59.58 to 394.37. Studies on hybrid vigor involving a greater number of crosses and more characters were made by Veatch (*46*). In 16 crosses the characters in which the hybrids exceeded, on the average, even the better parents, and therefore the characters in which hybrid vigor was shown, were the following: Number of pods per plant, plant weight, plant height, total stems and branch length, number of nodes, days from planting to flowering, seed weight or yield, and number of seed. Considerable variation, however, was found among the hybrids in the extent of hybrid vigor. Although the average of all the hybrids was higher in all characters studied than the average of all the parents, the average of all the better parents exceeded the average of the hybrids in average seed weight, number of seeds per pod, ratio of straw to grain, and average internode length.

Nagai (*22*) also reports that the individual of the first hybrid progeny is extremely prolific in comparison with its parents. In a cross between the Akazaya (seed yield per plant 34.18 grams) and the Hashikawa Yellow (seed yield per plant 34.18 grams) varieties, the first-generation hybrid yielded 52.97 grams and the first generation of the reciprocal cross 54.84 grams. In two other crosses similar evidences of hybrid vigor were shown in yield of seed over the parents. The problem of utilizing this hybrid vigor for increased production is rather complicated, and in order to make any definite progress more extensive investigations are essential.

INHERITANCE STUDIES AND CYTOLOGY[5]

The many strains differing widely in plant and seed characters and the almost complete self-fertility of the soybean make it an excellent plant for genetic study. The tediousness and difficulty of artificial crossing undoubtedly have been the chief reasons why more extensive genetic analysis of the plant has not been undertaken. Woodworth (*63*) and Nagai (*22*) have perhaps made the most substantial contributions. Considerable information has been collected on the behavior of progeny of natural and artificial hybrids, the most important features of which are presented herein under discussions of various plant and seed characters.

Plant Characters

Flower, stem, pubescence, and foliage

Soybean flowers occur in two colors, purple and white. While variations in intensity and grade of color occur in the purple-flowered varieties, no attempt has been made to differentiate them except by Nagai (*22*) and Takahashi and Fukuyama (*42*). Skvortzov (*33*)

[5] This section is written primarily for students or others professionally interested in breeding or genetics.

mentions a wild species of soybean with yellow flowers in Manchuria. This is perhaps an error, as there has been no hint of yellow flowers in the 10,000 or more introductions of cultivated and wild varieties and strains from all parts of the world, studied by the Department and numerous State experiment stations. In crosses, Woodworth (*58*) found purple (*W*) dominant to white (*w*), with a simple ratio of 3 purple to 1 white in F_2. A dihybrid ratio of 9 purple, 3 purplish red, and 4 white was obtained in an F_2 generation by Takahashi and Fukuyama (*42*). Nagai (*22*) reports purple dominant to white in a simple segregation ratio, or the segregations may be observed in three colors, purple, purplish blue, and white in a 9.3:4 ratio, the purple in the case evidently being determined by two factors. Piper and Morse (*31*), in both artificial and natural hybridization, found flower color to separate in simple Mendelian ratio, the purple flowers being dominant.

The stems of soybean seedlings are either purple or green, the purple color being most abundant just below the cotyledons. Purple-stemmed plants bear purple flowers and green-stemmed plants bear white flowers. In extensive tests at the Arlington Experiment Farm no exception was found to this relationship. Woodworth (*63*) reports similar results and states that the same gene probably is responsible for both characters. Stem color is undoubtedly a reliable indication of the flower color to be shown later by the plant.

According to Nagai (*22*), many Japanese varieties of edible soybeans have a special character known as fasciation (fig. 9). In crosses of such plants with normal plants, Woodworth (*63*), Takagi (*39*), and Nagai (*22*) found fasciation to be recessive, and in F_2 a ratio of 3 normal to 1 fasciated was obtained.

Nearly all varieties of soybeans are pubescent, that is, the stems, leaves, and pods are covered with fine tawny (brown) or gray hairs. In most cases there is no difficulty in distinguishing the two colors, but in some instances in selection from natural hybrids the pubescence color often is intermediate between gray and tawny, and sometimes both colors appear on the same plant. With artificial hybrids, the colors of pubescence have behaved in the same way as with natural hybrids. Tawny pubescence (*T*) is dominant to gray (*t*), and in F_2 a simple ratio of 3:1 is obtained.

Several yellow-seeded Japanese varieties, such as the Hadaka and Mizukuguri, are entirely glabrous, that is, lack pubescence or hairiness. These glabrous varieties of early, medium, and late maturity have been found by Japanese investigators to be highly resistant to attack by the pod borer (*Laspeyresia glycinivorella* Mats.), while pubescent varieties are highly susceptible to injury from this pest. In the United States, Johnson and Hollowell (*8*) found glabrous varieties subject to considerable injury from the leafhopper (*Empoasca fabae* (Harris)), while pubescent varieties were immune. According to Woodworth (*63*), glabrous soybeans fall into two distinct types. When crossed with pubescent varieties, one type behaves as a dominant while the other type behaves as a recessive. In each case the ratio is 3:1, indicating that a single factor pair is involved. Nagai and Saito (*23*) discovered the dominant type and Stewart and Wentz (*36*) the recessive. Glabrous soybean plants are smaller, shorter, and

Figure 9.—A, Stems and pods of fasciated soybean plants, *B*, determinate pod bearing type; *C*, indeterminate pod-bearing type.

yield less than most pubescent plants, according to Nagai and Saito (*23*) and Owen (*25*). Nagai (*22*) had one case in which strictly glabrous plants occurred in the F_3 generation in a cross of pubescent parents. The occurrence of this glabrous progeny was attributed to mutation.

In a study of the differences in amount of pubescence in American and Indian varieties, Woodhouse and Taylor (*54*) noted that the leaves of the Bengal "types I–V" differ from those of the Nepali "type VI" and the American varieties in being covered with soft upright hairs on their upper surfaces, whereas, the upper surfaces of the latter are covered with closely appressed hairs. In a cross between the cultivated and the wild soybean (*Glycine ussuriensis*), Karasawa (*9*) found appressed pubescence in the wild soybean dominant to erect in the cultivated soybean, the segregation occurring in accordance with the monohybrid ratio.

A wide variation occurs in the leaves of soybeans, involving shape, size, color, and degree of persistence. These characters merge by insensible degrees so that they are useful in differentiating varieties only in extreme cases. In shape the leaflets in some cases are ovate-lanceolate or almost linear; in others, nearly orbicular. In color they are usually a pale green but in some varieties dark green. In nearly all varieties the leaves commence to turn yellow as the pods begin to ripen and commonly all have fallen when the pods are mature. A few varieties, however, like the Medium Green, Old Dominion, Kingwa, and Wisconsin Black, retain their leaves until all or nearly all of the pods are mature. It has been quite generally observed that varieties with yellow cotyledons have leaves that turn yellow as they mature whereas some varieties with green cotyledons have leaves that remain green and persist until maturity. It is believed that the retention of green in the leaves is associated or tied up with the green cotyledon color and is separate and distinct from the simple retention of leaves by the plant. Additional leaflets occur not uncommonly in several varieties. This seems to be especially true with the linear-leaved form and with several early green-vegetable varieties from Japan, which frequently have leaves with four or five leaflets.

According to Nagai (*22*) there are two kinds of yellow leaves. One is greenish yellow from the beginning of growth and has little chlorophyll. The other has a normal or nearly normal amount of chlorophyll when young, but the leaves turn yellow as the plant grows. It was found that when either kind is crossed with a green-leaved variety, yellow leaves are recessive to green leaves, segregating in a 3:1 ratio in the former and in a 15:1 ratio in the latter.

Takahashi and Fukuyama (*42*), in studies of hybrids between normal and narrow-leaflet forms, found the F_1 generation to be intermediate, and in the F_2 a ratio of 1:2:1 was obtained. Woodworth (*63*) found essentially similar results in crosses between normal and narrow-leaflet forms, except that the broad shape was partially dominant and the F_2 generation was made up of two main forms, broad and narrow, in a 3:1 ratio. There were a few F_2 plants, however, that seemed to be intermediate in leaflet shape between the two parents.

In a cross made by Takahashi and Fukuyama (*42*) between a variety showing 73 percent of the compound leaves with extra leaflets and a normal variety the hybrid showed 52 percent of the compound leaves with extra leaflets. In the F_2, however, a ratio of 3 plants with extra leaflets to 1 normal plant was obtained.

Woodworth (*63*) found in the F_3 generation of a hybrid a single plant with variegated leaves. As neither parent possessed this character, it was supposed that the variegation arose as a mutation. In crosses with normal and variegated plants, variegation proved to be recessive. While the deviation from the expected 3:1 ratio was rather large, it was believed that variegation (v_1) is a simple recessive to normal in inheritance. Takagi (*39*) has reported a type with greenish-yellow leaves that appeared in one-sixteenth of the F_2 progeny of a cross between two normal, green-leaved plants.

Height of Plant and Maturity

Two cases of inheritance of size in the soybean plant have been reported in which definite segregation in plant height was observed. Woodworth (*58*) describes a natural hybrid that segregated in the ratio of 3 tall-growing plants to 1 short, stocky, early-maturing plant. Stewart (*34*) reports a dwarf form that behaved in inheritance as a simple recessive to the normal.

In soybeans there is a complete series of varieties ranging from very early (about 75 days) to very late (200 days or more). With very few exceptions earliness is correlated with size, the tallest varieties being latest. The maturity character usually has a complicated mode of inheritance because it is determined by numerous genes. Woodworth (*58*), however, describes a progeny of plants that segregated for two plant sizes, tall and short, in a 3:1 ratio. Coupled with plant size was a difference in maturity. The tall variety matured usually about 2 weeks later than the short variety. In this case, late maturity was dominant. Studies by Veatch (*46*) tended to confirm this, but Owen (*25*) found the F_1 of crosses between early and late varieties to resemble the early in time of maturity more than the late, and in F_2 the range in maturity due to segregation covered the entire parental range.

Pod-Bearing Habit and Pod Characters

In a classification of soybean varieties Etheridge, Helm, and King (*5*) placed 100 or more varieties into classes with respect to pod-bearing habit as determinate and indeterminate (fig. 9). The determinate class has a dense array of pods on the central stem, terminating in a blunt apex, with a thin dispersal on the lateral branches. The indeterminate class has a sparse and comparatively even distribution of pods over all branches and stems, a diminishing frequency toward the top of the central stem being notable. Woodworth (*63*) obtained a segregation for pod-bearing habit of 69 indeterminate plants to 19 determinate plants, a single-factor difference appearing to be involved.

The pods of the soybean exhibit a wide variation in color, ranging from very light straw yellow through numerous shades of gray and brown to black. As yet very little work has been done in classifying varieties as to pod color or in studying pod-color inheritance; however, pods usually have been divided into two groups—dark pods, which are

mostly black or nearly so, and light pods, ranging from a very light tan to light brown. In inheritance studies, Woodworth (*58*) and Piper and Morse (*31*) found dark pods dominant to light and in the F_2 obtained a ratio of 3 dark to 1 light.

While the pods in most varieties of soybeans are distinctly compressed, some are cylindric, and all possible intermediate forms exist. Nagai (*22*) places pods into two general classes, flat and bulky. In crosses he found the segregation of these two characters quite distinct, the flat (compressed) being dominant to the bulky (cylindric).

Soybean pods in most varieties contain two to three seeds, rarely one or four. The linear-leaf soybeans from Manchuria possess a large percentage of four-seeded pods, although a few five-seeded pods have been found. Without doubt, seed number per pod is a hereditary character, although in some instances it is quite unstable, depending upon method of culture, season, and fertility of the soil. Nagai (*22*), in a cross between two-seeded and three-seeded varieties, found that about 70 percent of the pods that segregated in the F_2 generation were two-seeded.

Under changeable weather conditions most soybean varieties tend to shatter their seeds readily. Some varieties, however, such as the Biloxi and Manchu, have been noted that hold their seeds better than others. The wild soybean shatters very easily and the Medium Green begins to shatter with the first mature pods. Piper and Morse (*31*), in a cross between the Medium Green and a glabrous nonshattering variety (F. P. I. No. 22876) from Japan, found the nonshattering character to be dominant to the shattering character of the Medium Green. Nagai (*22*) found in hybrid progeny of cultivated and wild soybeans that the shattering character was dominant to nonshattering, the segregation ratio in the F_2 being 3 shattering to 1 nonshattering.

Sterility, Growth Habit

As early as 1908, Piper and Morse (*31*) found small dwarflike plants, bearing few or no pods, in the different hybrid selections at the Arlington Experiment Farm. These plants were sterile or nearly so. Owen (*28*) describes a sterile strain in which both ovules and pollen grains were nonfunctional. This strain was found in a progeny of Manchu soybeans that segregated into 3 normal to 1 sterile, apparently a single-gene mutation being responsible.

All soybeans are strictly determinate as to growth, that is, the plants reach a definite size according to environment and then mature and die. The great majority of varieties are erect and branching with a well-defined main stem. The branches may be all short, or the lower ones elongated, either spreading or ascending. In other varieties the stems and branches, especially the elongated terminals, are more or less twining and usually weak, so that the plants are only suberect or even procumbent. The latter kind is represented by varieties from India and certain Siberian varieties of *Glycine gracilis*. The stem of the wild soybean (*G. ussuriensis*) is long and twining with a procumbent habit. Karasawa (*9*) in crossing experiments with the wild and cultivated soybeans found the F_1 hybrid of a twining nature. All of the plants of the F_2 and F_3 generations were more or less twining.

SEED CHARACTERS

Color of Seed Coat, Hilum, and Cotyledon

Most varieties of soybeans have unicolored seeds of straw yellow, olive yellow (greenish yellow), green, brown, or black. In some varieties straw-yellow seeds are very pale, especially when old, and they are sometimes erroneously called white, but no truly white seeds are known in soybeans. In straw-yellow varieties, the seeds have a greenish tinge if harvested before they are fully mature, which sometimes makes it difficult to distinguish them from varieties whose fully mature seeds are greenish yellow. Bicolored seed occurs in several varieties such as Black Eyebrow, Meyer, Taha, and Kura. The most common of the bicolored patterns is green or yellow with a saddle of black or brown, the latter not being sharply delineated. Some varieties have their seeds brindled brown and black, the two colors somewhat concentrically arranged. One variety has black seeds faintly marked with minute brown specks. On heterozygous plants the seeds are often irregularly bicolored and in some cases tricolored. Several black and a few brown varieties, with the outer layer of the testa broken by numerous cracks so as to expose the inner white layer, have been introduced from Chosen. In the case of the black-seeded and one or two brown-seeded introductions, this splitting has a net-like appearance that gives the beans a black-and-white or brown-and-white color.

Individual selections of natural hybrids by Piper and Morse (*31*) at the Arlington Experiment Farm gave some rather interesting results in the breaking up of the various seed colors. The selections with a single seed color, as straw yellow, black, or brown, broke up in simple Mendelian proportions, while those with more than one color presented a different ratio in the progeny.

Nagai (*20*) makes the following classification of soybeans according to color of seed coat:

(1) Beans producing no anthocyanin pigment in the seed coat.
(2) Beans producing anthocyanin pigment in the seed coat.

Owen (*27*) found the following classification of seed-coat color in soybeans most useful for the purpose of interpreting Mendelian characters:

(1) Self-color type.
(2) Bicolor type.
(3) Eyebrow pattern with green or yellow background.
(4) Green or yellow seed coat with dark hilum.
(5) Green or yellow seed coat with light hilum.

The genetic relationships of seed-coat colors and the effect of other genes on the colors have been studied extensively by Woodworth (*55*), Nagai (*22*), Owen (*27*), Terao (*43*), and Stewart (*35*). The inheritance of seed-coat color in soybeans differs somewhat from that of other members of the legume family. In soybeans, those seed-coat colors producing no plastid pigments as a rule mask those producing plastid pigment. The black pigment, according to Owen (*29*), is a very intense purple belonging to the general class of anthocyanins. The brown pigment is closely related to quercetin, and the green and yellow are plastid pigments.

According to Woodworth (*55*), the black and brown pigments are genetically independent of green and yellow in inheritance. Black is dominant to brown, and in F_2 a ratio of 3 black to 1 brown is obtained. Green is dominant over yellow, and in F_2 a ratio of 3 green to 1 yellow is obtained. When black or brown is crossed with green or yellow, the results are influenced by genes for inhibition of black and brown pigments over the seed coat. Owen (*27*) cites a case of incomplete dominance over brown. A natural hybrid was accidentally found that segregated according to a ratio of 3 black to 1 brown in the progeny that was grown, but all heterozygous plants bore seed slightly speckled with brown. It is believed that this brown speckling or flecking on the black seed coat is different from that symbolized by Woodworth (see table 2, symbol *Fl.*).

Varieties of soybeans exhibit a wide range of color types in the hilum, ranging from a pale-yellow or colorless hilum through various shades of brown to black. Two complementary genes for black pigment formation in the seed coat and hilum have been affirmed by Nagai (*22*), Woodworth (*55*), and Owen (*27*). The symbols for these genes were designated *C* and *L* by Nagai, *B* and *H* by Woodworth, and *R* and R_2 by Owen, the symbolism given by Owen appearing to be preferable according to Woodworth (*63*). In some early experiments which led to the suggestion of complementary factors for black hilum, Woodworth (*55*) obtained, in a cross between a strain with a black hilum and a strain with colorless hilum, black- and brown-hilum plants in the ratio of 9:7 He pointed out, however, that the ratio probably was 9 black: 6 brown: 1 colorless, because, on account of mottling of the seed coat, the plants having seed with brown hilums could not be easily distinguished from plants having seed with colorless hilums, and consequently they were classed together. Nagai (*22*) found in a cross between a plant having seed with a light-brown hilum and a plant having seed with a dark-brown hilum that the F_1 plants have slightly brownish seed and the F_2 may be dark brown, brown, and light brown in a 1:2:1 ratio. Woodworth (*63*), in crosses with parents of dark-brown hilum and light-brown hilum, found that the difference in the intensity of hilum color is due to the genes *T*, *t*, for tawny *v.* gray pubescence. Plants with *T* have dark-brown hilums, and plants with *t* have light-brown hilums. The genes for purple and white flowers (W_1w_1) have also been found to influence black and brown seed coat or hilum colors.

The cotyledons in the soybean are of two colors, yellow and green. When young the cotyledons are green, but in most varieties they turn to yellow toward maturity, while some varieties retain the original green. The behavior of the green and yellow cotyledons in natural and artificial hybrids has given some very interesting results. In 1909 Piper and Morse (*31*) noted in hybrid selection work that, with many plants having straw-colored to greenish-yellow seeds, seeds with green cotyledons and seeds with yellow cotyledons occurred on the same plant and sometimes in the same pod. These plants produced three kinds of progeny— those bearing only yellow-cotyledon seeds, those bearing only green-cotyledon seeds, and those bearing both kinds. The ratio was approximately 1:1:2, respectively, indicating that yellow was a simple Mendelian dominant to green. This

segregation in cotyledon color has been confirmed by Woodworth (*55*), who found evidence for two (duplicate) genes for yellow cotyledon. Terao (*43*) found in crosses that the cotyledon color of the hybrid progeny was the same as that of the female parent in every case and that there was no evidence of segregation in succeeding generations, indicating that cotyledon color in soybeans is maternal in inheritance. Maternal inheritance of cotyledon color in the soybean has been substantiated by Piper and Morse (*31*) and by Owen (*24*).

At least two kinds of transmission of the colors of the cotyledon are known. One is transmission through the maternal plant—that is, if the female parent is yellow the cotyledon of F_1 becomes yellow, and if it is green F_1 shows green cotyledons. Terao (*43*) suggests that there are two factors, *G* and *Y*, representing chlorophyll in two cotyledon colors. *G* is the one that always remains green and *Y* is the one that changes to yellow. In the other case of the inheritance of the cotyledon color, a simple Mendelian ratio has been obtained in F_2 in which yellow- and green-cotyledon seeds occur in a 3:1 or 15:1 ratio according as the parents differ by one or more genes.

Other Seed Characters

Defective or cracked seed coats have been observed by several investigators in black-, brown-, and yellow-seeded varieties and rarely in those having green seed. In some yellow and green seeds mottled with brown, the defects, or cracking, are found to occur mostly in brown areas. The character is undesirable, for in the defective or cracked areas the very thin inner coat cannot furnish the protection against unfavorable weather and disease organisms that is afforded normal soybeans in which the seed coat completely covers the seed. Stewart and Wentz (*37*), in a cross between the Wisconsin Black and Mandarin varieties, obtained in the F_2 51 normal to 5 defective or cracked, suggesting a 15:1 ratio. Nagai (*22*), in a cross between plants with normal and defective seed coats, found the defective or cracking character to be partially dominant. In F_2 a large number of individuals were produced showing different degrees of cracking, a rough estimate giving a ratio of 9 defective or cracked to 7 normal.

Nearly all varieties of soybeans have a comparatively smooth seed coat but differ more or less in the degree of smoothness. In some varieties the seed coat is rather dull in appearance, while in others it is bright and glossy. In the variety Sooty, some black and brown Siberian varieties of *Glycine gracilis*, and the wild soybean there is a distinct bloom covering the entire seed coat. The bloom can easily be scraped off, exposing the comparatively smooth seed coat underneath. In a cross between the Sooty and Manchu varieties, Woodworth (*63*) obtained a 3:1 ratio in the F_2 generation, while in another cross a 27:37 ratio was found in the F_2. In interpreting these ratios, he assumes that three genes, B_1, B_2, and B_3, are involved and that all three must be present together to manifest the bloom. If any one of these genes is not present, the character does not develop.

The range in size of soybean seed varies according to the variety, each variety having its own typical seed size. Varieties and introductions tested at the Arlington Experiment Farm ranged in average weight of 100 seeds from about 4 grams for the smallest to about

40 grams for the largest. Although seed size is mentioned in numerous published descriptions of soybean varieties, Nagai (*22*) and Takagi (*39*) are apparently the only investigators who have made studies of the inheritance of this character, the same results being obtained by both. In a cross of small seed (100 seeds=10.2 grams)×large seed (100 seeds=25.5 grams) Nagai obtained from the F_1 generation seed intermediate in size (100 seeds=14.2 grams). The segregation in the F_2 plants gave a wide range of variation between the seed sizes of the parent. Nagai states that it is very difficult to find plants bearing seeds of the same size as those of the larger plant and believes that many factors are involved in the inheritance of size of seed.

A considerable mottling of the seed of many yellow- and green-seeded varieties occupied the attention of plant breeders more than a decade ago. This mottling consisted of patches, blotches, or bands of black or brown pigment, irregular in outline and extent, superimposed on a ground color of yellow or green. Seeds with black hilums were mottled with black, and seeds with brown or colorless hilums were mottled with brown. In 1924 Woodworth and Cole (*66*) described the character and believed the cause to be physiological rather than genetical. After further studies, Woodworth states that the problem of mottling has some genetic aspects and also that a strain may be developed by selection that lacks the objectionable feature of mottling exhibited by the original variety. This is substantiated by selection of nonmottling plants from the Dixie variety, resulting in a pure yellow-seeded strain. Owen (*26*) concluded after an extensive investigation of this subject that mottling is due both to hereditary and environmental factors. In artificial hybrids the pubescence color was found in one instance to influence the extent of mottling, tawny pubescence increasing it, gray pubescence decreasing it. Owen, however, could not designate any particular factor as being the most important in causing mottling. The problem had certain genetic aspects, but the environmental effects were also quite evident. In recent years, mottling has not appeared to any great extent and it has been suggested that perhaps the wider use of varieties not subject to mottling has been an important factor.

Yield of Seed

In considering the most desirable character in varieties of soybeans, the most valuable single desideratum, as with other crops, is high yield of seed. Other characters of course are important, such as habit of growth, seed quality, color of seed, ease of shattering, etc., but extensive tests are being conducted at experiment stations in States where soybeans are an important crop to determine the best yielding varieties.

From the standpoint of inheritance, seed yield is a very complex character. The amount of seed produced is determined by heredity and environment (soil fertility, soil type, method of culture, and seasonal conditions). Woodworth (*63*), in studies of the yield character, has analyzed yield of seed into its component parts—number of nodes, number of pods per node, number of seeds per pod, percentage of abortive seed, and size of seed—and attempted to evaluate each variety studied with respect to these components. The general

situation was that any particular variety was found to rank well in one or more components and low or medium in others. No variety was found to rank highest in all. The conclusion reached was that the method of cross-breeding that has for its object the production of types with all yield components expressed to a higher degree than in the parents appears to be a promising method of breeding for increased seed yield in the soybean.

Disease Resistance

Although the soybean is attacked by a number of bacterial and fungus diseases, none of which reach serious proportions in oriental countries, no one disease as yet has caused serious injury to the crop in the United States. As cultivation continues, however, diseases undoubtedly will increase and assume more serious proportions. Breeding for disease resistance, therefore, may become an important factor in the improvement of the soybean. Studies of the various diseases of the soybean already found in this country indicate that varieties differ markedly in relative resistance to certain bacterial and fungus diseases.

Woodworth and Brown (*65*), in studies on varietal resistance and susceptibility to bacterial blight (*Bacterium glycineum* Coerper), found that field experiments indicated that soybean varieties vary greatly in their relative susceptibility to the bacterial blight. Of 48 varieties studied, about half were completely resistant, and the other half ranged from complete susceptibility to partial resistance.

A bacterial blight (*Bacterium sojae* Wolf) of soybeans was found on a number of varieties in North Carolina by Wolf (*52*). Studies failed to disclose any evidence of varietal resistance or susceptibility in any of the varieties.

Lehman and Woodside (*16*) made a very extensive study on resistance and susceptibility of soybean varieties to the bacterial pustule disease (*Bacterium phaseoli sojense* Hedges). After field observations and inoculations in greenhouse plantings, they were able to classify 56 varieties with respect to their resistance and susceptibility to the disease.

Extensive studies and experiments have been made on the mosaic disease of soybeans by Kendrick and Gardner (*13*). Results indicated quite clearly that varieties differ greatly in relative resistance and susceptibility.

"Brown spot" (*Septoria glycines* Hemmi), a fungus disease attacking the foliage of the soybean, has been studied by Wolf and Lehman (*53*), who noted differences among soybean varieties in relative resistance and susceptibility.

Another fungus disease, fusarium blight (*Fusarium bulbigenum* Cke. and Mass. var. *tracheiphilum* (E. F. Sm.) Wr.), was observed in North Carolina by Cromwell (*3*). In extensive variety tests, all varieties were found susceptible with the exception of the Black Eyebrow, which in two tests showed considerable resistance.

Lehman (*15*), in a study of another disease, frogeye leaf spot (*Cercospora daizu* Miura), attacking the foliage of the soybean, found that the early-maturing varieties in a certain group escaped serious injury while the late-maturing sorts suffered most.

Identification of Genes and Chromosomes

Several synonymic difficulties were encountered in establishing the identity of genes that different investigators have studied and designated differently. In cooperation with Woodworth and Williams, of the Illinois Agricultural Experiment Station, literature on the genetics of the soybean was reviewed thoroughly as to the genes of the soybean, and symbols were designated for each by the various geneticists. Liberty was taken in some cases to assign symbols to genes that have been studied but not named and certain symbols have been changed

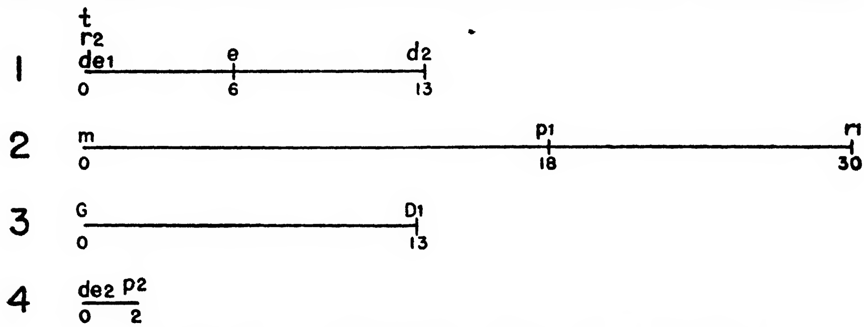

Figure 10.—Chromosome chart showing four groups of linked genes in soybeans. (Courtesy of C. M. Woodworth and L. F. Williams, Illinois Agricultural Experiment Station.)

(Woodworth, *63*) in order to bring them into line with current usage. Every effort has been made to make the list given in table 2 of the appendix as complete as possible, and it is hoped that the list given here will help to establish greater conformity in the designation of soybean genes in the future.

According to counts made by Karpetschenko, Kawami, Fukuda (Karasawa, *9*), and Veatch (*48*), the chromosome number in soybeans is given as 20 for the haploid and 40 for the diploid condition. The same number has also been counted in the wild soybean by Tschechow and Kartaschowa (*45*), as well as Fukuda (*6*). In F_1 hybrids between the wild and cultivated species of soybeans, Karasawa (*9*) found the same somatic chromosome number as in the parents. No abnormalities were found in the pollen mother cell in the course of sporogenesis, and the pollen therefrom was normal. Moreover, the fertility of the F_1 and its progeny was quite normal, indicating that the two species contain on the whole the same kind of genom.

Linkage studies in the soybean have not been very extensive, due largely, perhaps, to the difficulty of making artificial crosses. Woodworth, Nagai and Saito, Owen, and Stewart and Wentz have been the chief contributors to our meager knowledge of the association of genes in inheritance in the soybean. In table 3 of the appendix are shown the linkage groups reported up to the present time.

A provisional chromosome map of soybeans showing linkage relations of a few factors is given in figure 10. In chromosome 1, the gene order may not be as represented, since E and D_2 have not been studied together. In chromosomes 3 and 4, the order may be as represented or reversed.

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APPENDIX

Workers Identified With Soybean Improvement

United States

United States Department of Agriculture, Bureau of Plant Industry, Division of Forage Crops and Diseases:
- W. J. Morse, Washington, D. C.
- W. M. Stuart, Jr., and C. H. Binkley, Arlington Experiment Farm, Arlington, Va.
- J. L. Cartter, Urbana, Ill.
- M. G. Weiss, Ames, Iowa.
- J. L. Stephens, Tifton, Ga.
- T. F. Akers, West Point, Miss.
- R. E. Stitt, Statesville, N. C.
- H. A. Schoth, Corvallis, Oreg.

State agricultural experiment stations:
- Alabama, Auburn: H. B. Tisdale.
- Arkansas, Fayetteville: C. K. McClelland. Stuttgart: G. H. Banks.
- California, Berkeley: W. W. Mackie.
- Colorado, Fort Collins: D. W. Robertson, A. Kezer.
- Delaware, Newark: G. L. Schuster.
- Florida, Gainesville: G. E. Ritchey. Belle Glade: A. Daane. Quincy: J. D. Warner.
- Georgia, Athens: J. R. Fain. Experiment: R. P. Bledsoe.
- Illinois, Urbana: C. M. Woodworth, W. L. Burlison, J. C. Hackleman, L. F. Williams.
- Indiana, La Fayette: G. H. Cutler, R. R. Mulvey, K. E. Beeson, A. H. Probst.
- Iowa, Ames: H. D. Hughes, J. B. Wentz.
- Kansas, Manhattan: J. W. Zahnley.
- Kentucky, Lexington: E. J. Kinney.
- Louisiana, Baton Rouge: J. P. Gray.
- Maryland, College Park: J. E. Metzger, R. G. Rothgeb.
- Michigan, East Lansing: C. R. Megee.
- Minnesota, St. Paul: A. C. Arny, W. M. Myers.
- Mississippi, State College: W. R. Perkins, J. F. O'Kelly. Stoneville: H. A. York. Poplarville: J. C. Robert.
- Missouri, Columbia: W. C. Etheridge, C. A. Helm, B. M. King.
- New Hampshire, Durham: F. S. Prince.
- New Jersey, New Brunswick: H. B. Sprague.
- New York, Ithaca: R. G. Wiggans.
- North Carolina, Raleigh: C. B. Williams, R. L. Lovvorn.
- North Dakota, Fargo: A. F. Yeager.
- Ohio, Columbus: J. B. Park, P. Preston. Wooster: L. E. Thatcher.
- Oklahoma, Stillwater: B. F. Kiltz.
- Pennsylvania, State College: C. F. Noll, C. E. Myers.

South Carolina, Florence: E. E. Hall.
Tennessee, Knoxville: H. P. Ogden.
Texas, College Station: E. B. Reynolds.
Virginia, Blacksburg: M. S. Kipps. Williamsburg: R. P. Cocke.
West Virginia, Morgantown: J. A. Rigney.
Wisconsin, Green Bay: E. J. Delwiche. Madison: G. M. Briggs, B. D. Leith.

Foreign Countries

Australia:
- Department of Agriculture, New South Wales:
  - Glenn Innes: S. L. Macindoe.
  - Traftor: W. H. Darragh.
  - Richmond: N. S. Shirlow.
  - Sydney: H. Wenholz.

Canada:
- Central Experimental Farm, Ottawa: F. Dimmock.
- Dominion Experiment Station, Harrow: C. W. Owen.
- Agricultural College, Guelph: O. McConkey.

England:
- Royal Botanic Gardens, London: J. L. North.

Germany:
- Kaiser Wilhelm Institute, Manchberg: W. Rudorf.
- Südd. Soya-Institut, München: K. Baumeister.
- Soya-Institut, Mannheim: L. Müller.

Japan:
- Imperial Agricultural Experiment Station, Tokyo: H. Terao.
- Hokkaido Imperial Agricultural Experiment Station, Kotoni: V. Fujine, T. Hoshino.
- Saitama Agricultural Experiment Station, Ageo: T. Hasegawa.
- Central Agricultural Experiment Station, Suigen (Chosen): I. Nagai.
- Central Agricultural Experiment Branch Station, Shariin (Chosen): Y. Takahashi.
- Akita Agricultural Experiment Station, Akita: K. Adachi.

Manchuria:
- South Manchuria Railway Agricultural Experiment Stations:
  - Kungchuling: Y. Nakamoto, S. Tsuda, M. Ishikawa, K. Adachi.
  - Hsiungyocheng: K. Hisatake.
  - Kaiyuan: S. Kofuku.

TABLE 2.—*List of genes in soybeans*

Symbol	Dominant-recessive characters	Authority	Date published, observed, or reported
A	Appressed pubescence; a, erect pubescence	Karasawa	1936
B_1, B_2, B_3	Complementary genes for bloom on seed coat	Woodworth	1932
C_1, C_2	Complementary genes for cracking on seed-coat surface	Nagai	1926
D_1, D_2	Duplicate genes for yellow cotyledons; d_1d_2, green cotyledons.	Woodworth	1921
De_1	Normal seed coat; de_1, defective seed coat	Stewart and Wentz	1930
De_2	Normal seed coat; de_2, defective seed coat	Williams	1935
Df	Normal type; df, dwarf type	Stewart	1927
Dt	Indeterminate growth; dt, determinate growth	Woodworth	1923
E	Early maturity; e, late maturity	Owen	1927
F	Normal stem development; f, fasciated or flattened stem	Takagi, F	1929
Fl	Black seed coat flecked or speckled with brown; fl, self or solid black.	Woodworth	1930
G	Green seed coat; g, yellow seed coat	Nagai	1931
I, i^i, i^k, i	Multiple allelomorphic series responsible for inhibition of black or brown pigment in seed coat: I, Total inhibition; seeds show no black or brown pigment even in hilum. i^i, Partial inhibition; permits pigment only in hilum. i^k, Partial inhibition; responsible for Black Eyebrow pattern. i, No inhibition; seeds entirely black or brown.	Owen	1928

TABLE 2.—*List of genes in soybeans*—Continued

Symbol	Dominant-recessive characters	Authority	Date published, observed, or reported
L	Dark-colored or black pods; l, light-colored pods	Woodworth	1923
M	Responsible for black mottling on a self-brown seed coat; *m*, no mottling.	Nagai and Saito	1923
N	Normal hilum such as is found in most soybean varieties; *n*, abnormal hilum such as is found in Soysota variety.	Owen	1928
Na	Broad leaflet of most varieties; *na*, narrow leaflet	Takahashi and Fukuyama.	1919
P_1	Inhibition of pubescence, causing glabrousness; p_1, no inhibition.	Nagai and Saito	1923
P_2	Pubescence; p_2, no pubescence	Stewart and Wentz.	1926
R_1, r_1, r_1^o	Multiple allelomorphic series for seed-coat color *R*, complementary with R_2 for black seed coat or hilum. r_1, Complementary with R_2 for brown seed coat or hilum; recessive to R_1. r_1^o, reddish-brown seed coat; recessive to R_1 and *r*.	Nagai	1921
R_2	Complementary with R_1 for black seed coat or hilum; r_2, complementary with R_1 and w_1 for buff coat or hilum; r_2, R_1, and W_1, imperfect black.	Owen	1927
S	Tall, late-maturing type; *s*, stocky, early-maturing type	Woodworth	1923
Sh	Nonshattering of F. P. I. 22876, dominant to shattering of Medium Green; *sh*, shattering of Medium Green.	Piper and Morse	1911
Sh_2	Shattering of wild soybean, dominant to nonshattering of Kuradaizu; sh_2, nonshattering of Kuradaizu.	Nagai	1926
Sp	Spreading or fan-shape habit of growth; *sp*, erect compact habit of growth.	do	1926
St	Normal production of seed; *s*, sterility	Owen	1928
T	Tawny or brown pubescence color; *t*, gray pubescence color.	Piper and Morse	1910
V_1	Normal chlorophyll development; v_1, variegation	Woodworth	1932
W_1	Colored flowers; w_1, white flowers	Piper and Morse	1910
W_2	Complementary with W_1 for purple flower color; w_2 with W_1 gives purplish-blue flowers; w_1 with W_2 or w_2, white flowers.	Takahashi and Fukuyama.	1919
X	Extra leaflets in compound leaf; x, normal number, three	Nagai	1926
Y_1	Normal green plant; y_1, greenish-yellow leaves; weak plant.	do	1926
Y_2, Y_3	Complementary for green plant; $y_2\ y_3$, leaves turn yellow as plant grows; vigor fair.	do	1926
Y_4	Normal green plant; y_4, yellowish leaves; mutant found in Wilson-V.	Woodworth	1931
Y_5	Normal green plant; y_5, yellow-green leaves; mutant found in F. P. I. 65388; plant low in vigor.	do	1932
Y_6	Normal green plant; y_6, pale-green leaves; mutant found in Rokusun variety.	Williams	1936
Y_7	Normal green plant; y_7, leaves, stem, and pods become yellow as plant develops. Mutant found in Fuji	do	1936
Y_8	Normal green plant; y_8, yellow-green leaves in young plant, becoming green as plant develops.	Woodworth	1935

Table 3.—*Linkage of soybean characters*

Characters associated	Symbols	Percentage crossing over	Authority	Date published, observed, or reported
Green seed coat and green cotyledons	*G*, d_1	13	Woodworth Owen	1921 1927
Tawny pubescence and black seed coat or hilum color.	*T*, R_2	0	Woodworth	1932
Early maturity and tawny pubescence	*E*, *T*	6	Owen	1927
Defective seed coat and gray pubescence	de_1, *t*	0	Stewart and Wentz.	1930
Inhibition of pubescence and brown seed coat or hilum.	P_1, r_1	12	Owen	1927
Inhibition of pubescence and black mottling on a self-brown seed coat.	P_1, *M*	18	Nagai and Saito	1923
Pubescence color and cotyledon color	*T*, d_2	13	Williams	1935
Defective seed coat and pubescence	de_2, p_2	2	do	1935

TABLE 4.—*Soybean varieties: Origin and varietal characteristics* [1]

Variety	Origin	Year	Days to mature	Flower color	Pubescence color	Seed characters: Coat color	Germ color	Hilum color	Seeds per pod	Seeds per pound	Use
Agate	Introduction, Japan	1929	90	p, w	t	sy+br	y	br	2-3	2,816	gv
A. K.	Introduction, Manchuria	1912	110	p, w	g, t	sy	y	pa to bl	2-3	2,650	gra, f
Aksarben	do	1913	105	p, w	g	sy	y	y	2-3	2,675	gra
Arlington	Introduction, China	1908	125	p, w	g, t	bl	y	bl	2-3	4,750	f
Arksoy	Introduction, Chosen	1914	140	p	g	sy	y	br	2-3	3,136	f, gra
Avoyelles	Selection, Gray, Louisiana	1932	170	p	t	bl	y	bl	2-3	3,248	f
Bansei	Introduction, Japan	1929	110	p	g	sy	y	y	2-3	1,936	de, gv
Barchet	Introduction, China	1908	150	p	t	br	y	br	2-3	9,950	f
Biloxi	do	1908	165	p	t	br	y	br	2-3	1,875	f
Black Eyebrow	Introduction, Manchuria	1911	105	p, w	t	bl+br	y	bl	2-3	2,475	f
Cayuga	do	1925	100	w	t	bl	y	bl	2-3	3,632	f, gra
Chame	Introduction, Japan	1929	125	w	t	br	y	br	2-3	1,904	gv
Chernie	Introduction, Siberia	1906	100	p	t	bl	y	bl	2-3	4,675	f
Chestnut	Selection, Arlington Experiment Farm	1907	105	p	t	br	y	br	2-3	3,275	f
Chiquita	Introduction, China	1910	135	p, w	g	sy	y	br	2-3	4,050	f, gra
Chusei	Introduction, Japan	1929	110	w	g	sy	y	y	2-3	2,096	de, gv
Columbia	Introduction, China	1908	125	p, w	g	gr	gr	br	2-3	3,350	f
Creole	do	1927	165	p	t	sy	y	bl	2-3	3,120	f, gra
Delnoshat	Selection, York,[2] Mississippi	1925	165	w, p	g	sy	y	br	2-3	2,340	gra
Delsta	do	1925	150	w	g	sy	y	br	2-3	1,860	gra
Dixie	Selection, Arlington Experiment Farm	1914	135	p	g	sy	y	y	2-3	1,825	gra
Dunfield	Introduction, Manchuria	1913	110	p, w	g	sy	y	br	2-3-4	3,175	gra
Easycook	Introduction, China	1894	135	p	g	sy	y	br	2-3	2,700	de, gra
Ebony	Introduction, Chosen	1901	125	p, w	t	bl	y	bl	2-3	5,750	f
Elton	Introduction, Siberia	1906	105	p	g	sy	y	y	2-3	2,625	gra
Fuji	Introduction, Japan	1929	115	p, w	t	oy	y	bl	2-3	1,456	de, gra
George Washington	Selection, Clapp,[2] Virginia	1921	135	p	t	br	y	br	2-3	3,200	f, ns
Georgian	Introduction, China	1927	165	p	t	sy	y	pa to br	2-3	3,968	gra, f
Goku	Introduction, Japan	1929	110	w	g	sy	y	br	2-3	3,216	gv
Habaro	Introduction, Siberia	1906	105	p, w	g, t	sy	y	br	2-3	3,100	gra
Haberlandt	Introduction, Chosen	1901	130	p, w	t	sy	y	br	2-3	2,400	gra, de
Hahto	Introduction, Japan	1915	130	p	t	oy	y	bl	2-3	1,250	gv, de
Hakote	do	1929	115	w	t	oy	y	bl	2-3	1,440	gv, de
Harbinsoy	Selection, Arlington Experiment Farm	1922	120	w	t	sy	y	br	2-3	2,950	f, gra
Hayseed	Introduction, China	1927	160	w	t	sy	y	br	2-3	4,176	f, gra
Herman	Selection, Herman,[2] North Carolina	1915	135	p	t	sy	y	br	2-3	2,450	gra
Higan	Introduction, Japan	1929	135	p	g	sy	y	br	2-3	1,984	gv, de
Hiro	do	1930	115	w	t	bl	y	bl	2-3	1,312	gv, de

[1] bl=black; br=brown; de=dry edible beans; f=forage; g=gray; gr=green; gra=grain; gv=green-vegetable beans; oy=olive or greenish yellow; p=purple; pa=pale; sy=straw yellow; t=tawny; w=white.
[2] Name of breeder.

TABLE 4.—*Soybean varieties: Origin and varietal characteristics*—Continued

Variety	Origin	Year	Days to mature	Flower color	Pubescence color	Seed characters					Use
						Coat color	Germ color	Hilum color	Seeds per pod	Seeds per pound	
Hokkaido	Introduction, Japan	1930	115	p, w	g	sy	y	y	2-3	1,232	gv, de
Hollybrook	Selection, Wood,[3] Virginia	1902	135	w	g	sy	y	br	2-3	2,550	gra
Hongkong	Introduction, China	1908	120	p, w	g, t	sy	y	br	2-3	3,125	gra
Hoosier	Introduction, Manchuria	1911	110	p, w	g	sy	y	br	2-3	2,510	gra
Hurrelbrink	Selection, Hurrelbrink,[3] Illinois	1902	125	p	t	sy	y	br	2-3	2,800	gra
Illini	Selection, Woodworth,[3] Illinois	1921	105	w	g	sy	y	br	2-3	2,750	gra
Ilsoy	Selection, Smith,[3] Illinois	1913	120	p	t	br	y	br	2-3	3,250	f
Ito San	Introduction, Japan	1890	105	p	t	sy	y	y	2-3	3,325	gra
Jogun	do	1930	118	w	g	sy	y	y	2-3	1,360	gv, de
Kanro	Introduction, Chosen	1929	110	p	g	sy	y	pa to br	2-3	1,488	gv, de
Kingwa	Selection, Garber,[3] West Virginia	1921	125	p	g	bl	y	bl	3	3,808	f
Kura	Introduction, Japan	1929	118	w	t	bl+oy	y	bl	2	1,456	gv
Laredo	Introduction, China	1914	140	p, w	t	bl	y	bl	2-3	7,775	f
Lexington	Selection, Arlington Experiment Farm	1907	130	p, w	g	oy	y	br	2-3	3,585	f
Mammoth Brown	Selection, North Carolina	(1)	140	p	t	br	y	br	2-3	1,855	f, gra
Mammoth Yellow	Introduction, origin unknown	(1)	145	w	g	sy	y	br	2-3	2,150	gra
Mamredo	Selection, York,[3] Mississippi	1925	150	w	g	sy	y	br to bl	2-3	3,220	gra
Manchu	Introduction, Manchuria	1911	110	p, w	t	sy	y	, bl	2-3-4	2,350	gra
Mandarin	do	1911	100	p	g	sy	y	y	2-3	2,910	gra
Mandell	Selection, Cutler,[3] Indiana	1926	115	p	t	sy	y	bl	2-3	2,448	gra
Mansoy	Selection, Arlington Experiment Farm	1915	120	p	t	sy	y	bl	2-3	2,450	gra
Medium Green	Introduction, Japan	1889	120	p	t	gr	gr	br	2-3	2,485	f
Merko	Introduction, Siberia	1906	115	p, w	t, g	br	y	br	2-3	4,900	f
Midwest	Introduction, China	1901	115	p	t	sy	y	y to br	2-3	3,675	gra
Mikado	Selection, Parsons,[3] Indiana	1905	120	p	t	sy	y	br	2-3	3,086	gra
Minsoy	Introduction, France	1910	100	p	t	sy	y	br	2-3	3,700	gra
Monetta	Introduction, China	1927	165	p	t	sy	y	bl	2-3	2,976	f, gra
Morse	Introduction, Manchuria	1906	130	p, w	g	oy	y	br	2-3	2,500	f, gra
Mukden	Selection, Arlington Farm	1920	105	w	g	sy	y	br	2-3	2,750	gra
Nanda	Introduction, Chosen	1932	145	p	g	sy	y	pa	2	1,952	de, gv
Nanking	Introduction, China	1927	165	p	t	sy	y	br	2-3	5,600	gra
Norredo	Selection, unknown	(3)	125	p, w	g, t	bl	y	bl	2-3	5,856	f
Ogemaw	Selection, Evans,[3] Michigan	1902	90	w	t	br	y	br	2-3	3,125	f
Old Dominion	Introduction, China	1917	140	p	g	br	y	br	2-3	6,525	f
Oloxi	Cross, Wilds,[3] South Carolina	(3)	(3)	p	t	bl	y	bl	2-3	4,100	f
Osaya	Introduction, Japan	1929	115	w	g	sy	y	y	2-3	1,792	gv, de
Otootan	Introduction, Taiwan	1911	175	p	t	bl	y	bl	2-3	6,150	f
Ozark	Introduction, Chosen	1914	130	p	t	br	y	br	2-3	2,800	gra, f
Palmetto	Introduction, China	1927	165	p	t	sy	y	bl	2-3	3,408	gra, f
Pee Dee	Cross, Wilds,[3] South Carolina	(3)	145	p	t	bl	y	bl	2-3	5,100	f
Peking	Selection, Arlington Experiment Farm	1907	125	p, w	t	bl	y	bl	2-3	6,388	f
Pine Dell Perfection	Selection, Griesenauer,[3] Virginia	(3)	130	p	t	bl+br	y	bl	2-3	3,696	f

Pinpu	Introduction, Manchuria	1910	105	p	g	sy	y	br	2-3	2,675	gra
Rokusun	Introduction, Japan	1929	140	p	t	sy	y	br	2-3	1,584	gv, de
Sato	do	1929	115	w	t	bl	y	bl	2-3	1,488	gv
Scioto	Selection, Park,[2] Ohio	1925	120	p	t	sy	y	bl	2-3	2,960	gra
Shiro	Introduction, Japan	1929	115	w	t	oy	y	br, bl	2-3	1 632	gv
Sooty	Selection, Arlington Experiment Farm	1907	125	p, w	t, g	bl (dull)	y	bl	2-3-4	5,825	f
Sousei	Introduction, Japan	1929	115	p	t	oy	y	br	2-3	1,840	gv
Southern Prolific	Introduction, Chosen	1914	135	p	g	oy	y	br	2-3	2,350	gra
Soysota	Introduction, Italy	1910	100	p	t	br	y	br	2 3	4,900	f
Suru	Introduction, Japan	1930	115	p, w	g	sy	y	y	2-3	1,320	de
Tarheel Black	Introduction, China	1905	140	p, w	t	bl	y	bl	2-3	2,710	f
Toku	Introduction, Japan	1930	115	w	g	sy	y	br	2-3	1 952	de, gra
Tokyo	do	1901	140	p	g	oy	y	pa	2-3	2,260	gra, de
Virginia	Selection, Arlington Experiment Farm	1907	125	p	t	br	y	br	2-3	3 455	f
Waseda	do	1929	110	p, w	t	sy	y	pa to br	2-3	2,016	gv
White Biloxi	Selection, York,[2] Mississippi	1925	165	p	t	sy	y	br	2-3	2,230	gra
Wilson	Introduction, Manchuria	1906	125	p w	t, g	bl	y	bl	2-3	2,400	f
Wilson-Five	Selection, Arlington Experiment Farm	1912	125	p	g	bl	y	bl	2-3	5 025	f
Wisconsin Black	Selection, Wisconsin Agricultural Experiment Station	1898	100	p	t	bl	y	bl	2-3	3,085	f
Yelredo	Cross, Wilds,[2] South Carolina	([3])	165	p	t	sy	y	br	2-3	5,120	gra, f
Yokoten	Introduction, Japan	1907	130	p w	g	sy	y	br	2-3	2 175	gra

[2] Name of breeder

[3] Unknown

CLOVER IMPROVEMENT

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THROUGHOUT the world clover has been repeatedly referred to as the keystone of a permanent agriculture. Its introduction into agricultural use in the sixteenth century profoundly affected the entire system on which the old agriculture was based. As early as 1663, Yarranton wrote, in The Great Improvement of Lands by Clover, "for I perceive the land doth receive wonderful advantage by these leaves and branches; and as the leaves and branches, so the root doth very much contribute towards the enriching of the land." The improvement noted by Yarranton has been observed in every generation since that time, and to this has been added an increasing appreciation of clover as forage. Red clover, especially, is today the most widely adapted dual-purpose crop available to the farmer of the humid parts of the United States. Even older is the belief in clover as a lucky plant. Systematic attempts at improvement, however, are of recent origin.

Many plants have been called clovers, probably because of a similarity in usefulness and appearance to the true clover; but the true clovers and the sweetclovers only will be considered herein.

The true clovers belong to the genus *Trifolium*, of which there are some 250 described species of annual, biennial, and perennial forms that are widely distributed. In nearly every continent there are found indigenous species that occur only in that continent. In general they inhabit cool, moist regions or their growth is confined to the season of the year when cool climatic conditions prevail. Only four species—red (*Trifolium pratense* L.), alsike (*T. hybridum* L.), white (*T. repens* L.), and crimson (*T. incarnatum* L.)—are of primary importance and widely used, although several others are minor agricultural plants, in some cases of great importance locally.

Though recently considered a weed, sweetclover has had a phenomenal rise to the position of a forage crop of major importance in the United States. As an immigrant, it established itself along roadsides and railroad beds before its value was recognized. Sweetclover is now widely distributed over the world, but its native habitat appears to be in Asia Minor. Twenty species of sweetclover are recognized by Engler and Prantl. Three species—*Melilotus alba* Desr., *M.* [illegible]*lis* Lam., and *M. indica* All.—are of importance in agriculture.

RED CLOVER

OF THE true clovers, red clover (*Trifolium pratense*) is by far the most important. In the wild state it ranges over most of Europe and far into Siberia. The plant was known to be generally cultivated in the

Netherlands 370 years ago, and it is possible that there may have been a much older clover culture among the ancient Letts.

Natural Development

In the wild, red clover is an extremely variable plant. There are known to be early, late, smooth, hairy, prostrate, erect, and semierect forms. These forms can be found today, and it seems probable that one of them was the ancestor of the clover first used in agriculture, which was substantially like the double-cut clover of Europe today. The many varieties that have developed since the introduction of red clover into England in 1645 have resulted from the action of local conditions rather than conscious selection by man. Many such more or less local forms still exist, but they differ physiologically rather than morphologically; that is, they differ in resistance to cold and disease or in yielding ability rather than in characters that can readily be distinguished by the eye. In the Netherlands, however, a variety occurs, known as Maas, that is characterized by the almost total absence of the crescent-shaped white spot on the leaflets; and the character of rough hairiness readily distinguishes the American clover from its European progenitor.

Nothing is definitely known regarding the origin of red clover now common in North America. It is known that red clover was grown in Rhode Island in 1663 and that in later years there was a constant importation of seed from England. The American red clover is therefore certainly descended from the cultivated red clover of England, which in turn was introduced from Flanders. Just how the American form developed its characteristic hairiness is not known, but it has been surmised that it may have been because of the continued attacks

IN 1928 *the United States Department of Agriculture, through the cooperation of the State agricultural experiment stations, began a thorough search for red-clover stocks that had been grown continuously on the same farms or in the same communities for periods of 10 years or more without the introduction of seed from outside sources. These were planted in small observation plots and used as a basis for determining regional needs in red-clover-breeding programs for the humid Eastern States. It turned out that in the southern region red clover must be especially resistant to anthracnose; in the central region it must be both winter-hardy and disease-resistant; in the northern region it must be able to withstand a long period of winter dormancy; and in all regions resistance to powdery mildew is of varying importance. Breeding work based on these needs is now in progress, and some superior strains have already been introduced or are well advanced.*

of leafhoppers, which are common on clover and which prevent seed production in the smooth more than in the hairy plants. The English clover contains a certain percentage of hairy plants that, on this theory, would persist and hence gradually develop a hairy form (fig. 1).

Figure 1.—Stems of Italian red clover (*A*), American (*B*), and English broad red (*C*), showing the hairiness of American, believed to have been derived from the English by natural selection.

Classes of Cultivated Red Clover

In both Europe and North America the cultivated red clovers fall into two classes—(1) early, or double-cut, these giving two hay crops in a season; and (2) late, or single-cut, these giving but one hay crop in a season; and in most cases two or more forms are known in each class. Such forms are more numerous in the double-cuts than in the single-cuts and with a few exceptions are local or regional, rather than true varieties. Thus, in England, among double-cut clovers are the English Broad Red, Dorsett Marl, and Vale of Clwyd Early; among the single-cut clovers, Montgomery, Cornish Marl, English Late, and Vale of Clwyd Late. In the countries of continental Europe also, several regional varieties occur, distinguished by the name of the country or local area where the seed is produced, as Silesian, Hungarian, French, Italian, Swedish. Claims of superiority are made for all of these regional strains, and the evidence of comparative trials shows that in most cases each such regional variety is superior to others in the environment where it was developed. Some varieties,

as the Mattenklee of Switzerland, are reported by investigators to be especially distinguished by persistence.

These strains have not arisen as a result of conscious efforts toward improvement of clover, but are rather the products of different environments acting on a highly variable plant. It seems probable also that in some cases, as in England, natural crossing with the native wild red clover may have affected the progeny of the cultivated form first introduced from the low countries.

In North America regional strains are present as they are in Europe and differ in productivity, winter hardiness, and disease resistance. In the main, again, such characteristics have developed as a result of the action of local environments. In many States these strains have been grown continuously for 15 to 40 years without being mixed with other seed and have in many cases proved themselves decidedly superior. It must not be thought, however, that just because seed was grown in a certain State it has taken on a special character. A given lot of seed may represent one generation or many, and the trade names "Ohio", "Michigan", etc., have little significance.

Improvement Work in the United States

Definite attempts at the improvement of clovers are of relatively recent origin. In the United States studies looking toward the selection of a superior red clover have, at one time or another, been started at several State agricultural experiment stations, but, with the exception of the Tennessee anthracnose-resistant strain, such work has never been brought to fruition. The Kentucky station has found a superior strain that is called Kentucky 101, but it did not result from conscious selection but rather is an old stock grown for many years under the same environmental conditions. Similar valuable stocks exist in other States and can doubtless be made the basis for future breeding work.

In 1906 the Tennessee Agricultural Experiment Station selected a red clover resistant to the attacks of the fungus *Colletotrichum trifolii* S. M. Bain (fig. 2). Here again the form arose through the elimination of susceptible plants—man aided by seizing the opportunity to preserve a character brought out by the environment. The same process of selection, with perhaps less conscious human aid, has probably taken place elsewhere, since lines of long standing, highly resistant to this disease, are found in Kentucky and Virginia.

In 1928 the United States Department of Agriculture, through the cooperation of the State agricultural experiment stations, began a thorough search for red clover stocks that had been grown continuously on the same farms or in the same communities for periods of 10 years or more without the introduction of seed from outside sources. Approximately 75 strains or lots were secured, many of which had been grown for a continuous period of 40 years. These were planted in small observation plots, in cooperation with the Kentucky, Ohio, and Iowa Agricultural Experiment Stations. As a result of these studies and previous observations on the adaptation of foreign and regional strains of red clover, three regions of adaptation have been recognized in the humid eastern part of the United States, namely, the southern, central, and northern.

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The chief limiting factor to which the plants must become adapted in the southern region is disease, such as that caused by southern anthracnose (*Colletotrichum trifolii*). In addition the plants must be able to survive frequent great changes of temperature during the winter months, and high summer temperatures. This southern region is composed of the States of Tennessee, Kentucky, and Mary-

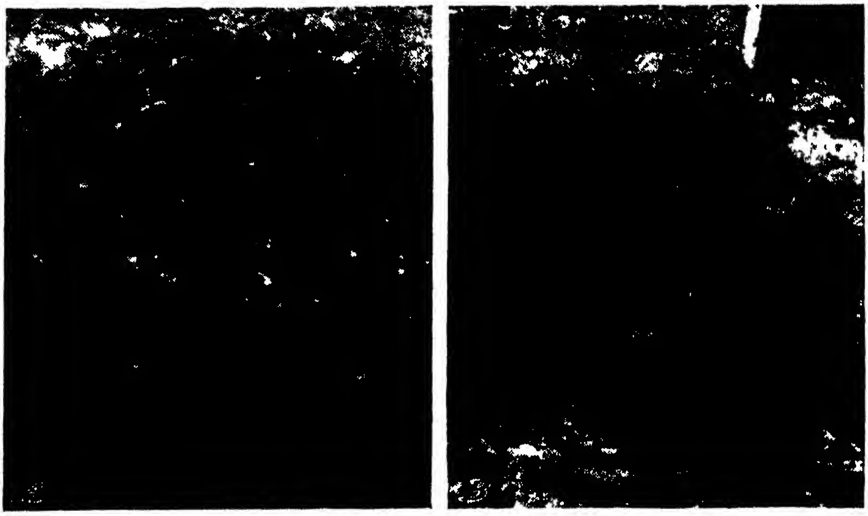

Figure 2.—Strains of red clover resistant and susceptible to southern anthracnose, caused by *Colletotrichum trifolii*: *A*, Tennessee anthracnose-resistant strain; *B*, Italian red clover. Arlington Experiment Farm, Arlington, Va.

land; the piedmont area of North Carolina and Virginia; parts of New Jersey; the southern parts of Ohio, Indiana, and Illinois; and a section of Missouri.

The central region includes the territory north of the southern region to approximately the latitude of the Illinois-Wisconsin boundary. Red clover adapted to this region must be disease-resistant and winter-hardy, since low temperatures with little snow protection are often met.

The northern region extends from the Wisconsin-Illinois line to the Canadian border. In this region no serious diseases are encountered, but the plants must be capable of tolerating a long period of dormancy, which at times may be accompanied by very low temperatures.

Throughout the three regions attacks of the powdery mildew fungus (*Erysiphe polygoni* DC.) and the potato leafhopper (*Empoasca fabae* Harr.) occur regularly with fluctuating intensity. In general the injury produced by the clover root borer (*Hylastinus obscurus* Marsham) is one of the principal causes of red clover killing-out during the second winter. In each of these regions the severity of the adverse factors varies from season to season and according to location.

After several years of study of the old strains in the central region of the red clover belt, superior strains were selected as a basis for

breeding studies. Several hundred plants of each of 10 strains were studied, and it is of interest that the percentage of superior plants in these strains ranged from 22 to 58, indicating the need of improvement.

In cooperation with the Kentucky station, seed of Tennessee anthracnose-resistant and Kentucky 101, two superior strains, was planted under controlled conditions, and the plants were artificially

Figure 3.—Resistance of red clover to the powdery mildew disease, caused by *Erysiphe polygoni: a*, Seedling plants from commercial seed, covered with mildew; *b*, seedling plants from mildew-resistant lines. University of Wisconsin, Madison, Wis., 1935.

inoculated with spores of southern anthracnose (*Colletotrichum trifolii*). In these tests the percentage of resistant plants of Kentucky 101 and of Tennessee anthracnose-resistant were, in 1925, 57 and 41, respectively, while only 10 percent of the plants of an old strain from Wisconsin remained alive.

In cooperation with the Wisconsin station, studies are in progress to develop lines resistant to powdery mildew (*Erysiphe polygoni*). Several lines have been developed that are resistant to two physiologic forms of the fungus (fig. 3). Both self-fertile and self-sterile mildew-resistant lines have been developed, but all of these are lacking in vigor and require further selection and hybridization.

Investigations on the improvement of red clover are in progress at the Minnesota, Pennsylvania, Tennessee, Indiana, New Jersey, and Idaho stations, and at the Kentucky, Wisconsin, and Illinois stations in cooperation with the United States Department of Agriculture.

Improvement Work Outside the United States

Attempts to develop improved clovers are being made in nearly every country in Europe and also in Australia and New Zealand.

In Canada two double-cut forms and two single-cuts are the result of deliberate selection. The Ottawa selection, the result of a mass selection process begun by the late M. O. Malte and carried forward for many years by the late R. I. Hamilton, is claimed to be of superior winter hardiness and is now coming into general use in Ottawa. An early or double-cut strain, called the Dollard, of superior winter hardiness, has been produced by J. N. Bird at MacDonald College, Quebec.

The Altaswede red clover, selected by G. H. Cutler from a Swedish strain, is said to be widely used in Alberta, but being a smooth clover it is not satisfactory for use in the eastern United States. The Manhardy, another smooth strain of single-cut, was selected at the Manitoba Agricultural College by W. Southworth out of various escaped and cultivated lines and is believed by Canadian authorities to be the hardiest strain of red clover in Canada.

In England the firm of Sutton & Sons selected a clover the seed of which was pure yellow instead of purple or yellow and purple. The stock came from yellow seed picked out of Chilean red clover. The effort to place the variety on the market was abandoned, however, since it was found impossible to prevent crossing in the field, and the purple color again appeared in the seed.

The firm of Gartons, Ltd., in England, began development work as early as 1890, but nothing of value has resulted from these efforts nor from the efforts of other private workers. Since the establishment of the Welsh Plant Breeding Station, systematic work has been undertaken on the study of red clover. Breeding of red clover under the direction of R. D. Williams has been important. So far one improved variety, S–123, has been offered to the public. This was released in 1936 and is believed to be useful for 2- and 3-year meadows. The following strains, built up through crossing various lines, are being tested but have not been released: S–87, S–106, S–110, and S–141.

Work of a similar kind has been undertaken in the Irish Free State, but results are not yet available. In New South Wales, Australia, an effort is being made to select a more persistent type out of a local strain known as Santhia. In New Zealand a strain known as Runciman's red clover is said to be truly perennial and of great value in pastures.

Martinet, and later Lindhard, tried to produce a variety with a short tube or corolla. Lindhard (1921) claimed that honeybees visited this variety freely and that it produced seed abundantly.

In Denmark various selected strains have been introduced as being more valuable than the local parent stocks. These are Øtofte early, semilate, and late. The Øtofte late was selected from a local strain of red clover. The strain called Øtofte semilate was bred from

Hersnap, another improved late clover used in Denmark. There is also Tystofte 40, a late form, and others.

In Germany various attempts have been made at improvement, notably at Bonn-Poppelsdorf, but no record has been found regarding results. Among private breeders was A. Dreger, who commenced his work in 1908 and produced violet-seeded and yellow-seeded varieties. According to Nessler (1931) the only bred clover in use in Germany is Original Lembke's red clover. This is an early red clover developed by Lembke in Wismar.

In Sweden such local strains as Norrum, for dry conditions; Karaby, produced by L. Karaby; and Mardal, said to be resistant to *Sclerotinia*, have become locally established. The experiment stations have also introduced Svalöf Purebred red clover, produced by H. Witte, and Mercur red clover, produced by N. Sylven, both of these strains being valued for yield and resistance to *Sclerotinia* and *Tylenchus*. Mercur was developed by mass selection from a local strain called Spannard. Weibwell's Smaragd, out of a Finnish local strain, and Göta Red, out of middle Swedish strains, are also in use. The improvement work in Sweden has been carried on by mass selection following intercrossing of various Swedish strains, or by mass selection out of a single strain.

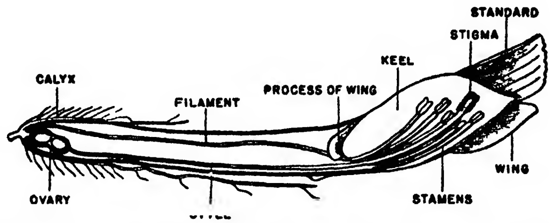

Figure 4.—Longitudinal section of a red clover flower, showing how anthers and style lie in the keel. (From Stebler and Schröter, The Best Forage Plants, pl. 24, fig. 2.)

F. Chmelar, of Brno, in correspondence, advises that original Dregers, out of Bohemian stock, and Mattenklee Rekord, selected by K. Holy out of Swiss Mattenklee, are bred varieties grown in Czechoslovakia.

In the Union of Soviet Socialist Republics special attention has been paid to native strains of wild red clover. These wild strains are said to vary in earliness, winter hardiness, production of aftermath, leafiness, and resistance to disease. The opinion is held by Lissitzyn and certain other Russian workers that these wild red clover strains rather than selections from existing cultivated forms should be made the basis of improvement.

Fertility and Pollination Relationships

Red clover heads are composed of from 50 to 150 florets, which in themselves are complete units of reproduction. The florets develop and open in an ascending order from the base to the top of the head. The pistil is usually curved, the stigma extending beyond the anthers, though florets have been found in which the style was greatly shortened, thus placing the stigma deep in the corolla tube (fig. 4). The ovary of red clover has two ovules, one normally developing upon fertilization and the other aborting. Plants have been found with a high percentage of pods having two seeds.

The anthers shed their pollen in the bud stage shortly before the floret or individual flower of the head opens. At this stage the pollen does not scatter freely. After the floret is open the stamens and pistil remain in the keel, and the pistil becomes exposed only after the floret is tripped. When the pressure causing the tripping is released, the stamens and pistil return to the keel unless the floret is ruptured. Fertilization occurs from 18 to 50 hours after pollination, the time depending on the temperature. When the atmospheric temperature is high, fertilization occurs much earlier than when it is cool. The degree of success of pollination can be approximately determined 2 to 3 days after fertilization.

Figure 5.—**R. D. Williams, Welsh Plant Breeding Station, Aberystwyth, Wales, who has devoted much attention to the subject of fertility and sterility of red clover.**

Self-sterility in red clover has generally been recognized since Darwin caged plants to exclude bees. The more recent studies of Fergus of Kentucky, Kirk in Minnesota, and Williams in Wales have clearly established the fact that nearly all the plants are self-sterile. However, lines have been established that are homozygous or pure for self-fertility, and Johnson in Minnesota has inbred one line for nine generations without materially decreasing the self-fertility. One of Fergus' self-fertile lines maintained its self-fertility for six generations, after which the line was lost.

Self-sterility in red clover is due to the slow growth of the pollen tube in the style, the ovules disintegrating before the generative nucleus reaches the egg. Recent investigations by Williams (fig. 5) in Wales indicate that this phenomenon is controlled by a series of many sterility alternative genes or allelomorphs. Whenever the same sterility factor is present in the pollen and in the female plant, growth of the pollen tube is inhibited. He has also shown that in self-fertile lines of red clover the presence of a noninhibitory self-fertility factor or gene permits the pollen tube to grow at the same rate as it does in the case of pollen from an unrelated plant.

Self Fertility

It is true that upon self-fertilization many red clover plants do produce a few seeds, but there is a distinct incompatibility in the succeeding progeny and the line cannot be maintained beyond the second or third generation. This phenomenon may be called pseudo-self-fertility as distinguished from true self-fertility.

Self-fertilization in red clover is accompanied by a decided decrease in vigor of the plants. This decrease is most pronounced in the first

and second generation and differs in different lines. Apparently Johnson's inbred line in Minnesota has maintained more vegetative and reproductive vigor that any other.

The number of true self-fertile plants in red clover is relatively small. Out of many hundred self-pollinations only a few self-fertile lines have been secured, though a large number of pseudo-self-fertile lines have been found. In connection with red clover breeding studies in the Department of Agriculture, from a spaced population of approximately 4,000 plants, 500 superior open-pollinated plants were selected; each of these 500 plants was self-pollinated, but not a single true self-fertile progeny was obtained.

Pollination

The structure of the red clover floret prevents cross-pollination by wind, since the anthers and pistil remain enclosed in the keel unless artificially tripped (fig. 4). Under natural conditions pollination is done by insects, nearly all of which are bees (order Hymenoptera). The bumblebees (*Bombus*) and the honeybees (*Apis*) are the principal pollinators, although at certain times and places bees of other genera, such as the ground bees (*Tetralonia* and *Melissodes*) and the leaf-cutter bees (*Megachile*), contribute to cross-pollination.

Bees visit the red clover floret for nectar and pollen or both, tripping the florets and transferring pollen from plant to plant, thus constantly maintaining the condition of mixed inheritance in the species. Other insects, such as moths, are constantly seen on red clover heads, but they do not come in contact with the pollen and therefore do not effect cross-pollination.

There has been considerable controversy as to the extent to which pollination can be accomplished by honeybees. Discussion has centered upon the fact that the tongue of the honeybee is not long enough to reach the nectar. The literature on this subject is voluminous and cannot be reviewed here. More recent investigations clearly indicate that honeybees visit red clover principally for pollen and seldom obtain nectar, but regardless of what is obtained, pollen is transferred and cross-pollination is effected.

Breeding Methods

In the breeding of red clover inherent difficulties exist that have greatly retarded advancement in the improvement of this crop. These factors are chiefly the small size of the red clover floret and the fact that the plants are self-sterile. In general the method followed in the past in breeding for an improved variety of red clover has been to start with a valuable local stock and attempt to secure a better strain by mass selection of the most desirable types. Because of the necessity for cross-pollination, red clover is in a hybrid condition and the progeny of selected plants will continue to produce a certain percentage of undesirables. These may be eliminated in some cases by continued selection and in others by unfavorable factors in the environment. The latter is the case with the anthracnose-resistant strains produced in the southern region of the red clover belt and the winter-hardy strains of the northern region, since they are naturally subjected to disease or to severe winter conditions. All varieties successfully

established in the United States and Canada to date have been developed by the aid of this natural selection.

Special inoculation beds with favorable conditions for development of the disease organisms have proved to be advantageous in studies on disease resistance. Experience has shown that field inoculations are not always successful, and there is always the possibility that surviving plants may have escaped inoculation rather than that they are resistant. The worker must also consider the susceptibility of the host as related to age and environment.

In details, the method of making crosses varies with the individual investigator. Toothpicks, camel's-hair brushes, cards, and crooked needles have all been successfully used for the transfer of pollen. Since most of the red clover plants are self-sterile, reciprocal crosses can readily be made without the emasculation or removal of anthers necessary with many plants.

Bumblebees from which pollen has been washed have been successfully used by Williams for cross-pollination, and this method offers the distinct advantage of securing large numbers of seeds in any specific cross. Lindhard caught queen bumblebees in the spring and developed the broods in special boxes that could be moved to cages in which the plants were enclosed. Natural nests have been transferred to artificial domiciles and moved about at will in studies by the Bureau of Plant Industry. Honeybees have been successfully used when many plants were to be cross-pollinated.

Williams (*17*),[1] of the Welsh Plant Breeding Station, follows three methods: (1) Strain building—selecting superior plants of old stocks and combining them by controlled crossing; (2) brother-and-sister matings—combining desirable sibs of the same families for several generations, eliminating plants with undesirable recessive characters after each crossing, and later outcrossing to unrelated families that have been sib-crossed; (3) dialed crossing—intercrossing several lines with one another to determine the combinations producing the best progenies, followed by intercrossing among such progenies to form a new strain.

The development of mildew-resistant lines in Wisconsin has resulted from selections made from artificially inoculated beds. The progeny of these selections were sib-crossed and selfed to secure lines homozygous or pure for mildew resistance. The crossing of unrelated lines resistant to mildew is in progress to restore vigor.

The results of studies by Williams and by the Bureau of Plant Industry clearly show the effects of sib-crossing. Loss of vigor with succeeding sib crosses for several generations is usually evident. Whether full vigor can be restored and maintained by combining a limited number of unrelated lines remains to be proved. Experience has shown that the growing of large populations of spaced plants is essential if progress is to be made. While controlled crossing may be accomplished in the field, a greenhouse is a valuable asset. The necessary manipulation can be more easily performed and a higher percentage of seed may be expected in the greenhouse than in the field.

The isolation and use of self-fertile lines in the breeding of red clover, while discredited by some investigators as offering little promise,

[1] Italic numbers in parentheses refer to Selected References, p. 1211.

has the distinct advantage of developing plants that are pure (homozygous). The loss of vigor by making sib crosses for several generations is practically as great as that resulting from selfing, and self-fertile lines are more readily maintained. The selfing of one head per plant is sufficient to determine whether it is self-fertile.

Isolation of Breeding Material

In Europe the problem of isolation of stocks in the early stages of development has been met by planting in an isolated field among other plants. Lang planted his red clover in the midst of a field of other plants blooming at the same time so that the bees might work on these plants first and thus have any foreign red clover pollen cleaned off before they arrived at the red clover plants. Dreger isolated his breeding stock in a field of *Vicia villosa*. By this means he claims to have produced a strain of red clover with uniformly violet seed.

Williams and Evans found that contamination by extraneous pollen depended on two factors—(1) the distance separating the bred strain from other red clover plants and (2) the profusion with which the strain flowers. In their experiments it was found that when there was little bloom on the pure strain the percentage of contamination was great, no matter how well isolated the plot. On the other hand, with abundant bloom relatively little contamination occurred even when the plot was not well isolated.

WHITE CLOVER

White clover, a common inhabitant of lawns, pastures, and roadsides, is widely distributed in every continent of the world, with a natural distribution probably as great as that of any other plant of the legume family. Moist and cool situations are its most favorable habitat and under such conditions growth is continuous. Though it is believed not to be indigenous to North America, it was brought over very early and the year of its introduction is not known.

The white clovers of agricultural value have been grouped as wild, cultivated or Dutch, and Giant or Ladino. Five other varieties are mentioned but are only of botanical interest.

In form these groups differ chiefly in plant size, the English wild white clover being smaller in all vegetative parts than the Dutch, and this again smaller than the Ladino. In England the wild white clover differs also in being more persistent than the Dutch white clover, which is often short-lived. As a group, the native or wild white clover is distinguished from the Dutch white clover and the Ladino white clover by the presence of a cyanophoric glucoside. This is an organic substance present in many herbage plants and which in the course of digestion forms hydrocyanic acid. The quantity present in white clover is small and harmless. The more persistent plants have a high glucoside content, while the short-lived Dutch and the Ladino have but little or none.

Origin of Varieties and Forms

The development of varieties and strains of white clover has resulted from the action of environment on this variable species. Thus in the United States it is possible to distinguish the strain produced from

Louisiana seed from that produced from Wisconsin seed, the Louisiana strain being more persistent under summer conditions but slightly less winter-hardy than the Wisconsin strain.

White clover was introduced into New Zealand from England, but the best white clover produced as wild white in New Zealand today differs from the wild white of England in its larger growth.

In New Zealand, where intensive work has been done with white clover, Bruce Levy has distinguished four strains of New Zealand white clover, differing in productivity and persistence, the best strain being like English wild white clover and the least satisfactory form like Dutch white clover. In Denmark two distinct varieties of white clover are grown, Morsø and Strynø. Of these the Morsø appears to be the more permanent and the better seed producer, but the Strynø is the better yielder of herbage. In Sweden a very persistent strain called Svea has been produced at Svalöf and is now on the market. In Finland the Tammisto strain, which has proved hardy and a good yielder, has been developed from native Finnish stocks.

Though no critical studies have yet been made, observations indicate that the white clover growing in old pastures in the northeastern United States has the same growth habit and persistency as the English wild white clover. A common descent may be presumed, since white clover was brought to this country by the early settlers.

Ladino white clover was first discovered in northern Italy, but its exact origin is unknown. It does well under irrigation but has not been successfully established in the eastern United States.

Breeding Investigations

The difficulties experienced in the breeding of white clover are similar to those in the breeding of red clover, and the same procedure is applicable. White clover, like red clover, is extremely variable in leaf size, color, and markings; flower and seed color; size of runners; and persistence. Combinations of one or more characters in individual plants have been observed from time to time. In many cases these have been perpetuated by vegetative propagation, and in a few cases strains have been developed that are homozygous for certain characters. All the strains to which reference has been made are the result of natural selection with only incidental help from man.

At present special breeding work is being conducted at the Weraroa station in New Zealand, where the Weraroa strain was isolated as no. B–95. It is said to be truly perennial and a good yielder. At the Welsh Plant Breeding Station a variety, S–100, was released in 1936 and is described as being more productive than commercial white clover and as lasting longer. It was produced from Dutch, New Zealand, and wild white clover and is intended for use in 1- to 3- year meadows. Another variety, S–99, has not yet been released. Breeding work is also being carried on at various stations in Germany, Denmark, Czechoslovakia, and Sweden.

Experiments by Williams (*17*), Erith (*3*), and others have clearly shown that self-sterility in white clover is not so marked as in red clover but is the result of a similar phenomenon. The possibility of developing self-fertile lines is, therefore, slightly greater. A pro-

nounced reduction in vigor results from inbreeding, with the appearance of dwarf and chlorophyll-deficient seedlings and other recessive characters.

OTHER TRUE CLOVERS

Crimson Clover

Crimson clover—the most important winter annual of the true clovers—was first introduced in the United States in the early part of the nineteenth century, and the Patent Office made a distribution of the seed in 1855. This species is self-fertile and is less variable than the clovers previously discussed. The florets are not self-tripping and for maximum seed crops require insect visitation.

Several varieties of crimson clover are recognized, differing in date of bloom and in color of the flowers. Vilmorin-Andrieux & Cie., of Paris, refer to Extra Early Crimson, Early Crimson, Late Crimson, Very Late White Flowering, and Extra Late Crimson Flowering. A difference of 4 to 5 days in time of maturity is shown between each of these varieties in the order named. An early white variety is also said to exist.

In the United States a local strain, developed in northern Georgia and known locally as Pitt's clover, is said to have given better results in Georgia than commercial seed.

Alsike Clover

The first recorded introduction of alsike clover into the United States occurred about 1839, when the Genesee Farmer, an agricultural journal, made a small distribution. No recognized varieties exist, but regional strains give varying results. In Sweden the native strain yielded more than that from Silesia or that from North America. In preliminary studies in the United States, differences of this sort have been noted. The plants are generally self-sterile, though Wilson in Minnesota has shown that self-fertility exists; loss of vigor follows inbreeding.

Subterranean, Berseem, and Persian Clovers

The clovers known as subterranean, berseem, and Persian are all annuals, the first two distinctly winter annuals, and are used for hay or grazing. Subterranean clover is little used in the United States. In Australia several strains of subterranean (*Trifolium subterraneum* L.) differing chiefly in date of maturity, are known, and in Egypt and elsewhere three or four distinct strains of berseem (*T. alexandrinum* L.) are recognized. Strains of Persian clover (*T. resupinatum* L.), differing in maturity, have been selected by workers in Turkistan. In none of the other true clovers are strains recognized, and no special improvement work, so far as known, is being carried on with these.

SWEETCLOVER

Although a relatively new crop, sweetclover offers one of the most promising possibilities for forage improvement. The different species appear on the whole to be self-fertile, although some are not self-pollinating. Large numbers of honeybees visit the florets, effecting a certain amount of cross-pollination and thus increasing variation among the plants.

In general, the sections where sweetclover is principally grown are the north-central region and the Great Plains States. This territory may be divided into two areas of adaptation—(1) the area east of the Nebraska-Iowa boundary and (2) the Great Plains States. In the eastern region resistance to a disease complex is of first importance in connection with the development of more palatable late-maturing strains for pasture. In the Great Plains States diseases as yet are of minor importance, but drought-resistant palatable strains for hay and pasture are needed. A coumarin-free strain would be desirable everywhere, since the presence of coumarin affects the palatibility of the herbage and, as shown later, is probably related to the development of a toxic substance in spoiled hay.

The sweetclovers grown in the United States belong to the genus *Melilotus*. They include white sweetclover (*M. alba*), yellow sweetclover (*M. officinalis*), and sourclover (*M. indica*). Redfield yellow, an early introduction of the United States Department of Agriculture, appears to be *M. suaveolens* Ledeb., though in many respects it resembles *M. officinalis*. The first species mentioned includes both biennial and annual forms, while *M. indica* is an annual, and of *M. suaveolens* and *M. officinalis* the biennial form only is known.

Varieties

Of the white sweetclover group, the Grundy County, Hubam, Arctic, Alpha, Iowa Late White, Ohio Evergreen, and Madrid White varieties have characteristic qualities and are in use to a greater or less extent. Grundy County White was first noted in Grundy County, Ill., in 1917, but is of unknown origin. It is early, of erect habit, with slender stems, and it is not so tall as the common biennial white sweetclover. Arctic was named by J. Bracken at the University of Saskatchewan, Saskatoon, Canada, and was derived from a Siberian importation brought in by N. E. Hansen. It is especially noted for winter hardiness and behaves as a dwarf variety in the central part of the United States, although making a much greater growth in Canada.

Madrid White, introduced by the United States Department of Agriculture through seed received from the Botanic Garden in Madrid, Spain, is a large-growing variety characterized by early seedling vigor and tolerance of the first year's growth to frost. Hubam is an annual mutation from *Melilotus alba* and was first brought to general attention by H. D. Hughes, of Iowa, in 1917. This variety resembles common biennial white sweetclover, except that it blooms and seeds freely the season of planting and does not survive a second year.

Alpha sweetclover is a variety developed by L. E. Kirk at the University of Saskatchewan. The first plants were found in a field of Arctic sweetclover in 1924, and Kirk developed the variety by a process of inbreeding and selection. The plants of the Alpha variety branch profusely at the crown, the slender stems being leafy and resembling alfalfa. It is a dwarf variety in the central part of the United States and is not adapted to that region.

Iowa Late White is a large-growing, late-maturing selection made by the late F. S. Wilkins, in 1935, at the Iowa Agricultural Experiment

Station, from a lot of seed secured from an Illinois farmer. Ohio Evergreen is similar in growth habits and maturity to the Iowa Late White. Selections of this variety were made by J. B. Park, of the Ohio Agricultural Experiment Station, as a result of several years of mass selection of desirable types secured from roadside plants. A selection made by the Illinois Agricultural Experiment Station and called Illinois No. 8 is another late-maturing uniform strain selected from wild plants. Selections made by Brink at the University of Wisconsin were developed in the effort to improve disease resistance. Hayes, Johnson, and Doxtater, of the Minnesota station, have made selections from Alpha and commercial white, resulting in a strain called Minnesota No. 1 and a strain of Alpha that is more disease-resistant than Alpha from Canada. In the Pacific Northwest the growing of sweetclover west of the Cascade Mountains was unsuccessful until the development of a strain resistant to what is believed to be stem rot. This variety was developed by H. A. Schoth, at Oregon Agricultural Experiment Station, over a period of years, by growing successive generations in the same soil, allowing the disease organism to eliminate the susceptible plants.

Figure 6.—L. E. Kirk, Dominion agrostologist, Dominion of Canada Experimental Farm, Ottawa, Canada, who has pioneered in the genetics of sweetclover.

Less attention has been given to the selection of varieties from yellow sweetclover (*Melilotus officinalis*) than from white sweetclover. In general, the varieties of yellow sweetclover are less productive and mature earlier than those of white sweetclover. Many varieties, such as Albotrea, Madison County or Switzer, and St. Louis Valley, are very much like the commercial yellow. Zouave, developed at the University of Saskatchewan, is more erect the first year than the commercial yellow and has seed that is densely mottled with purple. Daghestan Yellow, introduced from the Province of Daghestan, Transcaucasia, and having large and rounded leaflets, appears to be a form of *M. suaveolens*.

Redfield Yellow, a variety received by the Department of Agriculture from Manchuria in 1915 as *Melilotus alba*, but which later proved to be a yellow form, was developed and named at the Department's forage-crop field station at Redfield, S. Dak. The fact that Redfield Yellow crosses readily with *M. alba* while *M. officinalis* does not cross with *alba* and the further fact that Redfield Yellow does not cross with known varieties of *M. officinalis* appear to confirm the classification as *M. suaveolens*. Madrid Yellow, introduced by the Department from seed received from the Madrid Botanical Garden,

has vegetative characteristics similar to those of Madrid White, previously described. The character of early seedling vigor makes both the Madrid Yellow and the Madrid White superior for Great Plains conditions, where early establishment is of the utmost importance. In addition to the above-mentioned varieties of both white and yellow sweetclover, other local strains

Figure 7.—Segregating sweetclover line, showing branched dwarf character in center, compared to normal growth on each side. Arlington Experiment Farm, Arlington, Va., 1936.

are in existence, developed largely by the continued growing of strains over a period of years.

Breeding Work in North America

Definite breeding work has progressed more in Canada under the direction of L. E. Kirk than elsewhere (fig. 6). Kirk has made extensive studies on pollination, selfing, and crossing. Improvement work in Canada has been directed toward "the production of winter-hardy, fine stemmed, leafy, disease resistant and more palatable sorts." Three methods are used—(1) isolation of desirable plants or of plant groups so as to provide for immediate increase of a superior form; (2) isolation of desirable forms through selection within inbred lines; and (3) hybridization, to combine the desirable features of the best inbred lines (fig. 7). Studies of variations in coumarin content of individual plants have given promising results. Lines have been selected that

appear to be approaching homozygosity for low and for high coumarin content.

The Wisconsin station, in cooperation with the Department of Agriculture, has been studying the relationship between coumarin and palatability and toxic properties of spoiled sweetclover hay. Results indicate that coumarin is intimately connected with the toxic principle and is one of the important factors in the palatability of sweetclover for pasturage. Hybridization experiments are in progress within and between lines of *Melilotus alba*, *M. suaveolens*, *M. officinalis*, *M. dentata* Pers., and other species.

At the Minnesota station various lines have been inbred for 4 years. In agreement with the work in Canada, selfing has not resulted in any material reduction in vigor in either common biennial white clover or Alpha. The development of a variety of low coumarin content and high yield is the objective of this work.

In Kansas, Washington, and Texas, and at Guelph, Canada, selection of desirable sweetclover lines is in progress. The Nebraska and Illinois stations, in cooperation with the Department, have established nurseries for selection and breeding looking toward the development of varieties having superior value. In West Virginia various selfed lines are being grown with a view to securing one that will thrive at a higher acidity level than that at which sweetclover now does well. The Idaho station reports the development of a sweetclover having purple seeds, a crown similar to alfalfa, and nonshattering pods. A report for 1934 stated that none of the purple-seeded types proved homozygous for this character and that the plants were segregating for numerous other characteristics.

Breeding Work Abroad

The Russians have been interested in the breeding of sweetclover, especially at the Institute of Plant Breeding, at the Black Soil Regional Plant Breeding Center, at the Maikop and the Detsko-Selo stations in the north Caucasus, and at Saratov. Both commercial varieties and native wild strains are said to be used, various forms having been isolated to serve as breeding stock. Attention is being paid to variations in coumarin content.

At the Kaiser Wilhelm Institut für Züchtingsforschung, Müncheberg, Germany, under the direction of M. Ufer, many thousands of plants from different sources have been grown and studied for relative freedom from coumarin. Of these, 51 individuals were selected. Among the species studied were *Melilotus alba*, *M. officinalis*, *M. wolgica* Poir., *M. dentata*, and *M. indica*. This work was reported in 1934, but no later information is available.

Pollination and Fertility

Pollination of sweetclover under natural conditions is effected principally by honeybees, except insofar as the species, varieties, or individuals are spontaneously self-fertilized. Various workers have studied this problem, but only a brief summary of the information as given by Kirk and by Kirk and Stevenson can be given here. While *Melilotus alba* is generally highly self-fertile, three groups have been recognized: (1) Plants in which nearly all florets produce seed without

manipulation—spontaneously self-pollinated and self-fertile; (2) plants that do not produce seed without manipulation—self-fertile but not self-pollinating; and (3) self-sterile plants. The varieties of *M. officinalis* are not spontaneously self-pollinated, but are not completely self-sterile as is commonly thought. When the stigmatic surfaces are scratched in selfing, some seed is formed, though the proportion is not so great as when the florets are open-pollinated. The Redfield Yellow variety is spontaneously self-pollinated and self-fertile, and this is also the case with many lines of *M. dentata*.

GENETIC STUDIES IN CLOVER [2]

With the advent of more extensive genetic studies of plants, an occasional investigator became interested in the inheritance of particular characters of red clover. For the most part, however, the inherent difficulties occasioned by the self-sterility of the species and the manipulation of the florets in making crosses discouraged the initial efforts. Until recent years the published reports of such investigations were principally confined to general statements of what appeared to be evident.

Red Clover

Flower and seed-coat color of red clover were the basis of most of the early observations. De Vries (*14*) described the selection of a line that in the fifth generation had a large proportion of leaves composed of seven leaflets. He also reported that white flower color was recessive to red, being inherited in a simple ratio.

In 1903 Fisher likewise developed lines in which 85 to 100 percent of the progeny had yellow seed coats and another line in which 86 to 99 percent had dark-violet seed coats. In 1912 Kajanus (*6*) studied a blue-flowered red clover plant and reported that blue was recessive, being inherited in approximately a 15:1 ratio. He also stated that red flower color was dominant over white. In 1921 Witte (*20*) reported finding a white seeded red clover in which the white seed was associated with white flower. When this plant was crossed with those having yellow seed, the F_2 generation segregated in a 3:1 ratio.

In any large population of red clover plants, many have a crescent-shaped leaf marking while in others no markings are evident. Gmelin's (*5*) studies in 1916 showed that the presence of leaf markings was dominant. His work also confirmed the report of Kajanus (*6*) that white flower color was recessive to red. Fruwirth also studied flower color, counting the number of plants producing white and red flowers. The more recent work of Wexelsen (*16*) on the presence and size of leaf spot, leaf color, anthocyan pigment and its presence in stems and stipules, flower color, and resistance to mildew indicates an increasing interest in the inheritance of characters of red clover. Nijdam (*11*) also investigated incompatibility, seed-coat color, flower color, chlorophyll difference, sterile stamens, and dwarfs. These studies include the occurrence, variation, and segregations of crosses. Segregation ratios were reported.

With the establishment of the Welsh Plant Breeding Station an orderly investigation of red clover breeding began. Experimental

[2] This section is written primarily for students and others professionally interested in breeding or genetics.

proof by Williams and Silow (*19*) of sterility and fertility relationships of red clover, mentioned in a preceding section, affords a basis on which genetic studies may proceed soundly. The comprehensive studies of Williams (*18*) on flower color clearly show the presence of additional epistatic recessive factors with linkage relationships to the sterility genes, a condition not unexpected when the characters of large populations are critically examined. Besides the characters mentioned above, many investigators have observed the occurrence of dwarf forms, chlorophyll-deficient seedlings, abnormal flower-head development, and other variations.

Cytology of Red Clover and Other Trifolium Species

With the increased interest in cytological study as related to genetics, and its apparent usefulness in interspecific hybridization, studies on chromosome number and morphology have been undertaken by a few investigators, notably Bleier (*1*) Karpechenko (Karpetschenko) (*7*), and Wexelsen (*15*). In the majority of cases these investigators agree on the number of chromosomes, particularly in the most important species. Differences of opinion exist, however, on some points, and additional studies, with improved methods, are needed for a clearer understanding. The basic numbers of chromosomes are seven and eight, with multiples thereof, but species belonging to a given subsection of the genus *Trifolium* do not always have the same number of chromosomes. Ascherson and Graebner record various alleged hybrids as having been found in Europe, but experimental interspecific crossing has invariably been unsuccessful. A table of chromosome numbers of all species of *Trifolium* for which data are available is presented in the appendix.

White Clover

Genetic studies on the inheritance of different characters of white clover are in the developmental stage. In a preliminary report on a few crosses made between several varieties, Erith (*3*) states that leaf color and flower color are inherited as a single-factor difference. Normal green leaves are dominant to purple, and pink flower color is dominant to white. Cytological studies by Wexelsen (*15*) on two varieties—English wild and Ladino—show no difference in the chromosome numbers. Those of Ladino are, however, much larger, though considerable variation in this regard exists between plants of the English wild white clover. In crosses between varieties, the chromosome size of the F_1 generation was found to be intermediate between those of the parents.

Sweetclover

As indicated in the preceding section, improvement of sweetclover has been principally concerned with the introduction and trial of various sweetclovers from the Old World. The occurrence of natural hybrids and mutations has stimulated interest in characters and their inheritance.

In breeding sweetclover, emasculation is necessary unless the female parents carry a recessive character that may readily be determined in the F_1 generation. Kirk's water-suction method for greenhouse studies

and Savage's automobile vacuum method for field emasculation, as described in the article on Alfalfa Improvement in this Yearbook, are ingenious devices that have been successfully used. In view of the numerous hazards in breeding work, the need of greenhouse facilities cannot be overemphasized. A plant generation can be grown in the greenhouse in the winter either by placing the young seedlings under continuous light or by freezing seedlings a few weeks old and then placing them under a long-day exposure. These methods have been successfully used by Kirk in Canada and by Johnson in Minnesota.

Cytological studies are necessary for intelligent plant breeding, particularly when interspecific hybridization is to be undertaken. The studies of Castetter, Elders, Clarke, Smith, Fryer (*4*), Chekov (Tschechow), and Cooper all show that the diploid number of chromosomes of the species studied is 16. The morphology of the chromosomes of all the species investigated appears to be similar, although those of the species of the subsection *Campylorytis* are smaller than those of other species.

The appearance of Hubam and of the Alpha form undoubtedly stimulated inheritance studies. Smith concluded from his studies that the annual character was dominant and counts of segregating progeny indicated a close agreement of a 3: 1 ratio. Elders, Kirk (*9*), and Clarke (*2*) have shown that the Alpha type is recessive to normal and is inherited in a ratio of 3 : 1. Clarke also reports the presence of a recessive spreading dwarf character and of two factors for pale-green seedling. Linkage between pale green and spreading dwarf is evident.

Using the F_2 and F_3 lines developed from a natural hybrid between *Melilotus alba* and *M. suaveolens* (Redfield Yellow), Kirk (*8*) reports that the inheritance of flower color is in close agreement with a three-factor hypothesis, two factors for cream, varying in intensity, together giving yellow, and a third factor that inhibits the action of factors for cream and yellow giving white. Segregations in several of the above lines, however, indicate a deficiency of yellow plants. Reference to seed-coat color has been the basis of determining whether seed is from *M. alba* or *M. officinalis*. Various workers have considered the clear seed coats of *M. alba* as a distinguishing characteristic differing from those of *M. officinalis* in which a varying percentage of seeds are flecked with purple. Kirk and Stevenson have reported the finding of speckled seed coats in a line of Alpha (*M. alba*). Previous crosses indicated that color markings are dominant over clear seed-coat color. Kirk and Armstrong (*10*) also describe a mutation characterized by a reduction of the size of leaf with a pattern dissimilar to normal. This abnormality is also expressed in size and pattern of corolla. The plants are dwarfed, self-sterile, and cross-sterile to pollen from normal types.

The characters in sweetclover are as diverse as in other plants; purple seed coats, green cotyledons, dwarfs, and chlorophyll-deficient seedlings, germinable seed not needing scarification, and floret abnormalities have already been observed.

Interspecific Hybridization

The fact that all species of *Melilotus* have the same basic number of chromosomes, supported by the occurrence of natural and artificial

hybrids between species, has encouraged the belief that interspecific hybridization may be successful. The reports of early botanists on the occurrence of natural hybrids have been summarized by Schulz (*12*) and later by Ascherson and Graebner in their systematic treatise on the genus *Melilotus*. These authors mention hybrids between *M. alba* and *M. altissima* Thuill, *M. alba* and *M. officinalis*, *M. altissima* and *M. officinalis*, and *M. officinalis* and *M. wolgica*. The authors describe these alleged hybrids as having characters of both supposed parents, but genetic data on the supposed hybrids are wanting. Kirk and Stevenson failed to obtain a single hybrid between crosses of *M. alba* and *M. officinalis*. In an experiment designed to favor natural crossing between a line of *M. alba* and its varieties and species of yellow-flowered sweetclovers, Kirk secured one hybrid with cream-colored flowers. This is similar to hybrids secured later from artificial crosses between *M. alba* and Redfield Yellow. Furthermore, reciprocal crosses between Redfield Yellow and Albotrea and between Zouave and Redfield Yellow failed to produce a single hybrid. Natural hybrids of the same nature, involving crosses between Redfield Yellow and *M. alba*, have been selected by Garver at Redfield, S. Dak., and at Arlington Experiment Farm, Arlington, Va. Sylven, in Sweden, reports a natural hybrid between *M. alba* and *M. officinalis*, selected from seed secured from Canada. It is possible that this hybrid may have arisen from the cross between *M. alba* and Redfield Yellow or the reciprocal. More recent work of Stevenson and Kirk (*13*) shows that hybrids can readily be secured by artificial cross-pollination between *M. alba* (Alpha) and *M. suaveolens* (Redfield Yellow). The evidence tends to the conclusion that, while *M. alba* and *M. officinalis* and *M. officinalis* and *M. suaveolens* are reciprocally sterile, *M. alba* and *M. suaveolens* are reciprocally fertile. Compatibility varies, however, between individuals, depending upon which species is used as the male or female parent. In several cases crosses between *M. alba* and *M. officinalis* and between *M. alba* and *M. dentata* have resulted in the development of pods and shrunken nongerminating seed. Efforts to dissect out hybrid embryos at an early stage of development and grow these to maturity in nutrient cultures have failed. Further attempts at interspecific hybridization are in progress at several places.

Intergeneric crosses between *Melilotus*, *Medicago*, and *Trigonella* have been attempted by Fryer (*4*) and by Stevenson and Kirk (*13*), but without success.

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APPENDIX

TABLE 1.—*Chromosome numbers of investigated species of the genus Trifolium*

Species	Bleier n	Karpetschenko $2n$	Wexelsen $2n$
T. albopurpureum T. and G.			16
T. alexandrinum L.			16
T. alpestre L.	8	16	
T. ambiguum M. Bieb.		16	
T. angustifollium L.		14	
T. arvense L.	7	14	
T. badium Schreb.	7		
T. campestre Schreb. = *T. procumbens* L.	7		
T. ciliolatum Benth.			16
T. dichotomum H. and A.			32
T. filiforme L.		14	
T. fragiferum L.	8	16	
T. fucatum Lindl.			16
T. fucatum virescens (Greene) Wex.			16
T. glomeratum L.	7		16
T. hybridum L.	8	16	16
T. incarnatum L.	8	14	14
T. lappaceum L.	8	16	
T. lupinaster L.		48	
T. maritimum Huds.		16	
T. medium[1] L.	[2] 48–49	[2] 80	
T. microcephalum Pursh.			16
T. minus Sm.[3] (*dubium* Sibth).	14		32
T. montanum L.	[4] 9	16	
T. obtusiflorum Hook.			16
T. obtusiflorum majus (Greene) Wex.			16
T. ochroleucum Huds.	8		
T. pannonicum Jacq.	[2] 48–49	[2] 130	
T. parviflorum Ehrh.		16	
T. pratense[1] L.	7	14	14
T. procumbens L.		14	
T. reflexum L.			16
T. repens[1] L.	14	32	32
T. resupinatum L.	8	16	
T. rubens L.		16	
T. scabrum L.		16	
T. spadiceum L.		14	
T. squarrosum L.		14	
T. subterraneum L.			16
T. thalii Vill.	8		
T. tumens Stev.		16	
T. variegatum Nutt.			16
T. wormskjoldii Lehm.			[3] 48

[1] Reports on additional chromosome counts: *T. repens*, $2n=16$, A. G. Erith. *T. repens*, $n=$about 12, J. N. Martin. *T. medium*, $2n=78$, J. N. Armstrong, Central Experimental Farm, Ottawa, Canada, by correspondence. *T. pratense*, $n=7$, J. Kawakomi. *T. repens*, $n=16$, J. Kawakomi.
[2] About. [3] Specific identity uncertain. [4] Uncertain, not enough material.

TABLE 2.—*Location, kind of clover, and past and present personnel engaged in clover improvement*

[An asterisk (*) designates workers whose salaries are completely or partly paid from Federal funds]

AMERICAN WORKERS

Location of workers	Kind of clover	Past personnel	Present personnel
Washington, D. C.	All clovers	A. J. Pieters,* H. S. Coe,* L. W. Kephart.*	E. A. Hollowell.*
Moscow, Idaho	Red, sweet, white	H. W. Hulbert	C. A. Michels.
Urbana, Ill.	Red, sweet	W. B. Gernert	C. M. Woodworth, D. Heusinkveld,* J. J. Pieper.
Lafayette, Ind.	Red		G. H. Cutler, R. R. Mulvey.
Ames, Iowa	Red, sweet	F. S. Wilkins,* S. N. Smith.	H. D. Hughes.
Manhattan, Kans.	Sweet		J. W. Zahnley.
Hays, Kans.	do	D. A. Savage*	
Lexington, Ky.	Red	L. Henson*	E. N. Fergus, W. D. Valleau.
St. Paul, Minn.	Sweet, red	L. E. Kirk, F. R. Immer, H. E. Brewbaker, C. W. Doxtater.	H. K. Hayes, H. K. Wilson, I. J. Johnson, W. M. Meyers.
Lincoln, Nebr.	Sweet		T. A. Kisselbach, S. Garver,* K. F. Manke.*
Brunswick, N. J.	Red, alsike, white		H. B. Sprague, E. M. Hodges.
Columbus, Ohio	Sweet		J. B. Park.
Corvallis, Oreg.	Sweet, crimson		H. A. Schoth.*
State College, Pa.	Red		H. B. Musser.
Knoxville, Tenn.	do	S. M. Bain, S. H. Essary.	C. S. Sherbakoff.
College Station, Tex.	Sweet		P. B. Dunkle.
Pullman, Wash.	do	V. B. Hawk	Ralph Weihing.
Morgantown, W. Va.	do		C. R. Burnham.
Madison, Wis.	White, red, and sweet.	C. E. Yarwood	R. A. Brink, W. K. Smith,* O. F. Smith,* O. S. Aamodt, H. S. Ahlgren, J. G. Dickson, F. Tinney.*

Table 2.—*Location, kind of clover, and past and present personnel engaged in clover improvement*—Continued

PARTIAL LIST OF FOREIGN WORKERS (COMPILED FROM REPORTS RECEIVED)

Location of workers	Kind of clover	Past personnel	Present personnel
Australia:			
New South Wales	Red, white, subterranean.		S. L. Macindoe, W. T. Atkinson.
Tasmania, Strathroy	Subterranean		R. H. Beyin, E. F. Fricke.
Victoria	Subterranean, white		J. E. Harrison, F. R. Drake, E. D. Cameron.
West Australia, Muresk Agricultural College.	Subterranean		T. C. Dunne.
Canada:			
Ontario:			
Ontario Agricultural College.	Red, white		O. M. McConkey.
Guelph	Sweet		
Dominion Experimental Farm, Ottawa.	Red	M. O. Malte, G. P. McRostie, R. I. Hamilton.	L. E. Kirk, J. M. Armstrong.
Saskatchewan, University of Saskatchewan, Saskatoon.	Sweet	S. Bracken, L. E. Kirk	T. M. Stevenson, W. J. White.
Quebec, MacDonald College.	Red	L. S. Klinck, L. A. Waitzengen, C. P. McRostie, A. MacTaggart.	J. N. Bird.
Wales:			
Welsh Plant Breeding Station, Aberystwyth.	Red, white, crimson		R. D. Williams.
Germany:			
Kaiser Wilhelm Institute, Berlin.	Red, alsike, white, sweet.		W. Rudorf, F. Hackbarth Schrock.
Netherlands:			
Agricultural High School, Wageningen.	Red		H. M. Gmelin.
Norway:			
Felleskjøpets Stamsaedgaard, Hjellum.	do		H. Wexelsen.
Apelsvoll, Toten	White		
Vagønes, Bodø	Red		
Union of Soviet Socialist Republics:			
Institute of Plant Industry, Leningrad.	do		Lissitzyn, Sinskaya.
Sweden:			
Sveriges Utsädesforening Svalof.	Red, white, alsike	H. Witte, G. Eriksson, B. Kajanus.	N. Sylen, G. Nilsson-Leissner, R. Torssell, R. Nilsson, J. E. Sidén, G. Eriksson, E. Akerberg.
Switzerland:			
Swiss Agricultural Experiment Station, Orlikon.	Red		A. Volkart.

VARIETAL IMPROVEMENT IN HOPS

D. C. SMITH, Formerly Agent, Division of Drug and Related Plants, Bureau of Plant Industry [1]

LUPULIN, a substance consisting of resins and essential oil, imparts to beer, ale, and other malt beverages their characteristic bitter flavor. The scales or bracts of the hop—which resembles a fir cone in its general makeup—possess small, yellow, granular bodies or lupulin grains, easily visible to the eye (fig. 1). These contain the resins and oil. The oil, contributing also to the aroma, is usually driven off in the boiling process but may be replaced later. Materials known as tannins occurring in the scales and stem of the cone aid in the clarification of the brew after boiling.

Each 31-gallon barrel of beer brewed in the United States requires only a half to four-fifths of a pound of hops, though abroad the figure sometimes reaches 1¼ pounds. Thus in spite of the extent of the brewing industry, the acreage of hops required is of minor importance agriculturally when compared with many crops. Hops are all-important to the brewers, however, since beer is made principally of malted barley, hops, and water. There are rather exacting requirements in quality of hops, and both yield and quality are determined by many influences. Breeding of better hops, therefore, becomes an undertaking of vital concern both to brewers and to growers.

In other countries attention has been given to hop breeding as a means of improvement for many years. Such work with hops in the United States is at its beginning, though much progress has been made in recent years in breeding other crop plants. Some of the back-ground of hop culture will help the reader to better understand the breeder's work.

USE OF HOPS ANCIENT IN ORIGIN

JUST when hopped beer was first made is not known. The Egyptians had a sweet-sour alcoholic beverage made like beer but without hops. Hops were apparently used by the Greeks only as a salad plant; even today young hop shoots are eaten like asparagus by some people. In early times hops were supposed to free the blood of "all impurities, tumors, and flatulence", cure the itch and other skin diseases, and "relieve the liver and spleen." Taken as a fresh vegetable, they may well have had some beneficial effect in the diet. Today individuals may be found who believe that sleeping on a pillow stuffed with dried hops somehow contributes to health.

[1] Previously in charge of hop-breeding investigations. The author is indebted to G. R. Hoerner, agent, Division of Drug and Related Plants, for collaborating on some parts of this paper dealing with pathology, and to Frank Rabak, associate biochemist in the same Division, for making the chemical and physical examinations and furnishing the data in tables 1 and 6

But the overwhelming utilization of hops has been in brewing, this use being first developed either in Russia or in Germany. German records go back to 768 A. D., in the time of Charlemagne, when King Pepin le Bref donated hop gardens to the monastery of St. Denis. Subsequently many monasteries became famous for their brews. By 1320–30 A. D., hopped beer was in general favor in Germany. Hop culture spread to the Netherlands, and John the Bold, Duke of Burgundy, founded a Knightly Order of the Hop. Late in the fifteenth century the plant was introduced into England, but Henry VII and Henry VIII liked beer without hops and prohibited their use. Swedish tastes were the opposite; an ordinance of 1440 required every farmer to grow 40 poles of hops. In Bohemia the Emperor Charles IV personally selected the spots most suitable for hop growing. Today leading producing countries abroad are England and Wales, Germany, Czechoslovakia, France, and Belgium.

Figure 1.—Branch of hop vine with mature, well-developed cone below and blighted, withered cones due to downy mildew above and to the side.

In North America, hop growing began in New Netherlands as early as 1629 and in Virginia in 1648, though it did not become important until about 1800. In 1808 the first hop yard was established in New York. In 1849 the New England States and New York produced nearly 1,500,000 pounds, of which New York grew 70 percent. After the Civil War the industry developed in Wisconsin, reaching a maximum of 25,000 bales[2] in 1869. In 1865, Oneida County, N. Y., produced 1,265,000 pounds, and in 1879 the State reached an all-time maximum of 21,629,000 pounds.[3]

The growing of hops on the Pacific coast was started between 1859 and 1869. Though New York was still the leading State in 1899, the production in Oregon and that in California each exceeded that of New York by 1909. In recent years hop cultivation in this country, except in Washington, Oregon, and California, has been negligible.

[2] Present commercial bales weigh approximately 200 pounds.
[3] Attention of the reader is called to the appendix at the end of this article, listing sources of information available.

In 1935 these three States harvested 47,746,000 pounds of hops on 38,900 acres. Slightly over half of the tonnage was grown in Oregon.

During the twenties hop growing in New York was practically wiped out by powdery mildew, but there is a revival of interest in that State, as indicated by the work recently begun by the New York (State) Agricultural Experiment Station at Geneva looking toward the improvement of hop varieties.

The growing of hops is somewhat similar to that of pole beans. The vines are trained on poles or pole-and-wire trellises, ordinarily 10 to 20 feet in height. Plants are spaced from 4 to 8 feet apart, the latter distance being most general on the Pacific coast. At harvest the vines are let down and the cones are picked by hand. The green hops are then hauled to drying houses, piled in bulk, and slowly dried with artificial heat for about 20 hours. Later they are compressed into bales of about 200 pounds each, sewn over with burlap, and the grower's part is completed.

Hops are long-lived perennial plants propagated by root cuttings and having a strong climbing habit. Curiously enough, the vines always wind in the same direction. New shoots are produced each year, and after harvest old growth is removed as in the case of cane fruits. Plants may be grown from seed, but they then exhibit great diversity in characters, many being strikingly inferior. Few growers have noticed hop seeds germinate. Hop plants possess remarkable vigor, young vines having been observed, under favorable conditions, to elongate 12 inches in 24 hours.

Hops are closely allied only to elm, mulberry, hemp, and nettles among the commonly known plants and are known to botanists as *Humulus lupulus* L. A native American type has been segregated as *H. americanus* Nutt. An annual ornamental variety called the Japanese hop (*H. japonicus* Sieb. and Zucc.) is a cousin, as is *H. neomexicanus* (A. Nels. and Cockerell) Rydb., a native sort found in

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BEER, *ale, and other malt beverages depend principally on hops for their characteristic flavors, and no satisfactory substitute has ever been found. Improvement of hops by breeding is, therefore, of vital concern to both brewers and growers. The attainment of a choice product is very difficult, since the hop plant is extremely sensitive to sun, wind, heat, rain, insects, and diseases, and the quality of the cone depends on type, color, soundness, aroma, and content of resins and essential oils. Breeding may play an important part in improving most of these characteristics. The varietal improvement program is new in the United States and though the hop plant is not easy to deal with, the progress made in developing superior varieties in Europe suggests what may be accomplished with sustained and active investigations.*

Colorado and vicinity. The first two species mentioned include all commercial hop varieties.

PECULIARITIES AND PROBLEMS IN HOP BREEDING

THE HOP is one of the few cultivated plant species in which male and female flowers are borne on different individuals. Since commercial hops are the dried and pressed cones from the female plants and these develop without fertilization, the males are not indispensable in commercial culture. The latter do serve to stimulate production of larger, heavier, and earlier maturing cones by the female plants (*20*).[4] Such hops contain seeds, which contribute to the weight but which have no value in brewing, and in parts of continental Europe the presence of male plants in yards is forbidden by law. In the United States and England about 1 male to 100 female plants may be grown.

To the breeder, seed production is necessary, since it is in seedling progenies that opportunity for selection of improved varieties is most promising. The breeding problem is closely analogous to that in dairy-cattle improvement. There is no method of determining the value of a sire in providing desirable heredity to obtain high-producing cows except by progeny tests, since milk production, like hop development, is a purely female character. Nevertheless, from a hereditary viewpoint, the male contributes markedly in each case.

BREWING REQUIREMENTS, YIELD, AND MATURITY

The characteristics of choice hops, from the brewmasters' viewpoint, are relatively few. They should possess a high soft-resin content, delicate aroma, and a clean, bright appearance, and contain few or no seeds, leaves, and stems. Because of the slow, gradual development and fragile nature of the cone, coupled with the extreme sensitivity of the plant to sun, wind, heat, rain, insects, and diseases, the attainment of a choice product is exceedingly difficult. Harvesting operations also play no small part in determining the quality of hops received by the brewery. Though much investigational work has been done in attempts to find suitable substitutes for hops, the use of this crop continues to be the only means in use of giving the desired qualities to beer.

In the culture of hops, the grower has many serious troubles. Most important among these are maintenance of yields, control of diseases and insects, standardization of high quality, and many minor difficulties arising from these. The first task of the breeder is to recognize and understand these factors.

The world over, yields of dry hops per acre may range from 300 to 4,000 pounds. While much depends on the country and locality, the variety used is of chief interest in this respect. The principal varieties of the Pacific coast are Late Clusters, comprising about 75 percent[5] of the acreage; Fuggles, about 15 percent; and Early Clusters, 10 percent. In good years, Late Clusters produce an average of about 1,500 pounds, Early Clusters 1,300 pounds, and Fuggles 1,100 pounds of dry hops per acre. Incidentally, yields in continental Europe are

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[4] Italic number in parentheses refer to Literature Cited, p 1239.
[5] Includes some Canadian Red vines.

usually from 600 to 1,100 pounds per acre while those of England and Wales approximate those of the United States.

Fuggles is the earliest maturing variety, usually being ready for harvest about August 20, with Early Clusters closely following. Ripening of Late Clusters, which is the main crop, begins in Oregon in early September. Maturity of hops is generally earlier in California and to some extent in the Yakima Valley of Washington. Harvesting of Late Clusters may extend into early October. Many growers have acreages of two or more varieties, which allows a longer harvesting season. Increased yields are always a breeder's objective and the period of maturity is of importance in most sections.

Downy Mildew, Scourge of the Hop Plant

Like other plants, hops are attacked by various diseases, the most serious of which, at the present time, is downy mildew. Other important troubles in the United States are blue mold or powdery mildew, sooty mold, which accompanies infestations of plant lice, and crown gall. Blue mold, a serious disease in England and to some extent responsible for the decline of hop production in New York, has not been reported on the Pacific coast. Sooty mold may be serious in any year when plant lice are prevalent. These diseases may attack hop cones, leaves, roots, or stems causing lowered quality or complete destruction. The effects of downy mildew on cone development are shown in figure 1. In addition to those mentioned, other minor diseases of various types have often been present in Europe and the United States.

In recent years hop growers throughout the principal hop-growing countries have been greatly concerned with downy mildew. Its ravages have resembled in many respects those of the late blight disease of the potato, which caused the Irish famine in 1845 and 1846, or of the frequent stem rust epidemics of cereals in the Middle West.

Downy mildew was first described in Japan in 1905. In 1909 it was observed in the United States, being found in Wisconsin. In 1920 minor attacks of the disease were seen at Wye, in Kent, England, but in 1921 it was not observed there. During 1922 and 1923 it increased in prevalence at Wye, and in 1923 it was reported in Germany and Czechoslovakia. Belgium and France reported it in 1924 and the Union of Soviet Socialist Republics in 1925. In 1926 it appeared in Italy. Beginning in 1927 serious losses were caused, England suffering damage estimated at nearly one-third of the crop and Bavaria also experiencing heavy losses. Some Bavarian growers sprayed 10 times during the season to control the spread of the trouble. Since 1927 the disease has appeared irregularly in Europe, but in individual localities losses may involve the entire crop. Weather conditions are important influences in the development of the disease.

Though found in Wisconsin in 1915, downy mildew did not cause economic losses in North America until 1928, when it appeared in New York, Manitoba, and British Columbia. In 1929 it developed extensively in western Washington and in 1930 was severe in western Oregon. The disease did not appear in coastal California until 1934 and in the Sacramento Valley until 1935. During 1936 it was prevalent in all areas where it had been found previously and caused

a marked reduction in the yield and quality of the crop. To date it has not been officially recorded as existing in the Yakima Valley of Washington, though experienced growers have reported traces of it.

While downy mildew appears irregularly, it has been estimated that 20 to 25 percent of the crop is annually lost through the depredations of this disease in the Pacific Coast States. The source of the organism causing downy mildew (*Pseudoperonospora humuli* (Miyabe and Tak.) Wilson) is problematical, but it is thought to be native on wild hops in the United States. The control of this devastating disease is perhaps the most important concern of hop producers both in the United States and in Europe and is a major objective of the breeder.

Quality and Other Considerations

Particularly in recent years, but more or less persistently over a long period, growers have been concerned with problems affecting quality. Considered from the variety-improvement viewpoint, items of importance are soft-resin content, aroma, and the existence of seeds. Commercially, hops are bought on the basis of general variety or type, color, aroma, lupulin content, and soundness. These might be termed "sight", "smell", and "touch" characters, and experienced growers and dealers rely greatly on these three senses. Recently resin content as determined by chemical analysis has become a greater influence in the hop trade.

Proper attention to the various steps in harvesting and curing favors quality to a large extent, but aside from this, variety and locality are also extremely significant factors. With respect to soft-resin content, American-grown hops are equal or superior to the best European lots. The latter are reputed to be preferable in aroma. Continental hops are also noteworthy for their freedom from seeds as compared with the English and American products. German and Bohemian hops continue to sell at a high premium over domestic lots in the New York markets. Though sufficient domestic production of hops for supplying the American trade usually exists, the use of a certain percentage of foreign hops for brewing is a general practice in this country. To improve the quality of domestic hops is thus another primary object of breeding efforts.

Insects affecting hops most frequently are plant lice or aphids and the red spider. These pests exist in both European and Pacific coast hop sections. Root borers, cutworms, flea beetles, and other insects occasionally do considerable damage. Aphids have been generally present and, where they are numerous, the secretion of honeydew, a sticky sweet substance, reduces quality and serves as a substratum for molds to develop. Red spiders affect the foliage mainly and are usually prevalent under conditions of slow growth and dry, warm weather.

In picking, hops that separate readily from the vines are harvested with the least crumbling and breaking. Types that tend to remain without disintegration in the complete processes of ripening, harvesting, and drying result in the best dried samples. Plants must be long-lived to keep down yard maintenance costs and maintain high yields.

EARLY DEVELOPMENT OF VARIETIES

The natural variability of the hop plant and the futility of attempting to propagate commercially by means of seed was recognized at an early date (*13*). In 1669, different types were distinguished, and by 1726 the existence of male and female plants was noted by European growers. Many varieties were known by 1799. The desirability of growing uniform sorts was also acknowledged though in England during the nineteenth century there was a great confusion of varieties.

During the development of the industry in the United States, as in Europe, many named varieties have been grown that, with the exception of the four now grown on the Pacific coast, have disappeared from commercial fields. Introductions of foreign types made from time to time by producers of extensive acreages have also vanished for the most part.

In the important years of production in New York several varieties grown included English Cluster, Grape, Canada Red, Palmer Seedling, and Humphrey Seedling. The latter types were also cultivated in California and in addition the so-called "American hop" was grown. The Fuggles variety did not prove popular in California.

The earliest recognition by the Department of Agriculture of the need of improved varieties of hops in the United States was in 1900, when David Fairchild imported roots of the best European varieties. After thorough tests it was found that these did not yield well enough to make their production under American conditions profitable. In 1904 he started breeding work and crossed European varieties with American male plants. Prior to this American hop growers had from time to time sought to accomplish the same purpose in the same way with similar results.

In 1908 Stockberger (*17*) outlined a program he had undertaken in the Department of Agriculture. He referred to the failure of the earlier attempts to adapt European varieties and suggested a different procedure based on a recognition of the fact that the hop plant is greatly influenced by soil and climatic conditions, so that improvement by selection of the best varieties already being grown in this country would be simpler and give quicker results. He proposed a careful study of the domestic varieties, the selection of promising individual seedlings, and thereafter the development of desirable types by hybridization. Although the chief objectives he sought related to productiveness and quality, he stated that individual hop plants had shown a marked resistance to disease and that these were being propagated to determine not only whether that character is transmittable but to note their general qualities from other standpoints.

Progress on this project was reported in brief statements in the Yearbooks of the Department of Agriculture for 1911 and 1912 in which the selection of several promising hybrid seedlings and the continued introduction of foreign sorts is referred to. By 1916 several thousand seedlings were under cultivation. About this time a number of circumstances forced the abandonment of the project. A reduction in funds made a continuation of the field work impossible. The European war interfered with further importations of foreign varieties, and a few years thereafter the advent of prohibition greatly reduced the commercial importance of hops.

The investigations of State experiment stations have not until recently been directed toward problems concerning hop varietal improvement, and early Federal experiments have not been continuous.

Principally because of the inroads of downy mildew, experimental work with hops was initiated in 1930 by the Division of Drug and Related Plants of the Bureau of Plant Industry, United States Department of Agriculture, in cooperation with the Oregon Agricultural Experiment Station. The principal purpose of the program was to investigate disease control through field practices and to work toward the development of improved, disease-resistant varieties. Experiments have been in progress since that time. More recently varietal improvement of hops has been started by the New York (State) Agricultural Experiment Station at Geneva, as previously mentioned.

In Europe there seems to have been from early times a careful selection of stocks, varieties appearing and disappearing frequently. Though the origins of many strains are obscure, numerous ones are known to have resulted from selection of chance seedlings and others by propagation from desirable plants. The Late Clusters variety is thought to have arisen from a chance seedling of the wild hop. The origin of Fuggles is typical of the development of many strains. Concerning it Percival (*6, p. 87*) wrote:

> The original plant was a casual seedling which appeared in the flower-garden of Mr. George Stace, of Horsmonden, Kent. The seed from which the plant arose was shaken out along with crumbs from the hop-picking dinner basket used by Mrs. Stace, the seedling being noticed about the year 1861. The sets were afterwards introduced to the public by Mr. Richard Fuggle of Brenchley, about the year 1875.

Another old English variety, Colgate, was started from a likely looking plant found growing in a hedge. Bates Brewer was developed from root cuttings obtained from an outstanding plant that was paid for in whisky (*6*). Many of the continental varieties undoubtedly began with similar plant selections. The varietal history of hops closely resembles that of potatoes. Selections of seedlings by growers, followed by vegetative propagation, have frequently originated new types in both plants.

Fruwirth (*4, pp. 77–88*) assigned the origin of several early varieties, including Golding, Early Brambling, and Semsch, to bud variations, the variants then being propagated independently by cuttings. This is comparable to the bud or graft propagation of new apple types appearing on trees of old varieties.

Individual workers, not growers primarily, undertook independent investigations late in the last century. Fruwirth began selection of promising individuals in 1888. Other workers mentioned by Fruwirth were Stambach, who first planted seedlings in 1894, and Remy, who in 1898 was making studies of the resins and tannins of seedlings. Early work also included that of Beckenhaupt at Weissenburg and Wagner at Weihstephan, Germany, who grew local and introduced varieties in comparative trials.

Organized efforts for hop improvement began fairly late in the last century. A testing garden was established near Saaz, Bohemia, in 1897, and many varieties were grown. Breeding by seedling selection had begun in Belgium by 1903. About 1898 the Agricultural College

of Wales began investigations on hop improvement, and breeding was undertaken in 1907. One of the oldest and most active investigational projects has been in progress in England since about 1904. In 1913 visitors to the college hop nursery at Wye, Kent, selected promising seedlings for trial and subsequently 2,830 cuttings from 23 varieties were supplied to growers. A testing station especially for determining brewing value was established at East Malling in 1917 and has made important contributions to the English work. By 1911 Denmark had begun variety investigations. Additional stimulation was given to hop breeding in Europe generally by the severe losses due to downy mildew in 1926 and 1927. In 1926 a society for hop research was founded in the Hallertau district of Bavaria. In 1932 a large German hop company placed its acreage at the disposal of the government for testing purposes. The work of hop selection in the Union of Soviet Socialist Republics, undertaken by the Agricultural Academy of Moscow, began in 1926. In addition to those mentioned, other state, governmental, and private agencies in Europe are concerned with varietal improvement of hops. In the appendix are listed some of the workers and the countries in which experimental work is in progress.

RECENT BREEDING WORK

The improvement of hop varieties concerns the cone-bearing female individuals particularly. When seeded hops are grown, male plants that produce abundant pollen at the time of the flowering of the female plants are needed. Thus selection of desirable male plants may be necessary.

Considering grower and trade demands, an ideal variety would embody resistance to downy mildew, high yield, suitable resin content, and good aroma. It would be medium leafy, easily picked, resistant to insects, and capable of remaining on the vines a reasonable time after maturity without deterioration. Excessive fragility and large stems would be undesirable. This indicates the varied character of the hop-breeding problem. Meanwhile, new diseases or other troubles may appear to provide additional complications. Considering all these points, no varieties commonly grown at present quite "fill the bill."

Recent work has developed along several important lines. In 1930 and 1931 an extensive survey was made of the plant material being grown in commercial yards of Oregon, to determine the possibility of selection of superior types in old hop yards. In 1935 a similar, though less comprehensive, inventory was made in coastal California. Superficial examinations have also been made of a few Yakima Valley yards in Washington. The general result of these surveys has been failure to find occasional plants, which might be propagated as improved types, strikingly superior to the general lots of the four important varieties. There has frequently, however, been a varying percentage of inferior sorts, the elimination of which would allow a sizeable increase in production. Such types have been chiefly hermaphrodites[6] and sterile plants producing no flowers, often called bastard hops by

[6] Hermaphrodites, as in animals, are individual plants developing both male and female sexual characters. In hops such plants produce pollen and also cones.

growers. In many yards male plants are unnecessarily numerous for pollination purposes. Additional work is being done on vegetative selection among commercial varieties and the breeder is constantly watching for superior individuals.

In all plant improvement one of the most promising methods of obtaining better types is the introduction of varieties from foreign

Figure 2.—Vines of the Late Clusters variety of hops, with side branches covered with glassine bags to control pollination. Bags are held in place by paper clips, and operations are recorded on small marking tags attached to the stems.

countries having growing conditions comparable to those in our own hop areas. Experience has not been promising as to the value of this practice in hop improvement, but it is hoped that useful breeding material will be acquired by this means. Beginning in 1931, attempts have been made to obtain propagation stock of superior English and continental varieties to grow in the experimental nursery at Corvallis, Oreg., in comparison with domestic sorts. Though some European countries have prohibitions against the exportation of cuttings, in all about 35 foreign strains have been obtained by the Division of Plant Exploration and Introduction and are now being grown. Cuttings for propagation improperly packed are perishable and in some instances difficulty has been experienced in obtaining living roots shipped long distances. Plants from imported cuttings do not usually bear hops until the second year.

The third method of attack that may be used for variety improvement is the selection of superior plants from those grown from seed. This plan appears to offer most promise. Since it is difficult to designate male individuals according to variety, all seeds produced may be considered of hybrid nature. Thus seed may be collected from any good female in the hope that some of the progeny will excel the

mother plant in various characters. The nature of the male parent in such a case is unknown. It is also possible to obtain seeds from plants that have been pollinated artificially. In these cases the nature of the male is known, and vigorous, desirable types may be used. When controlled pollination is practiced, the female flowers are covered with

Figure 3.—View of experimental yard showing plant variation among hop seedlings. Those in the foreground are superior types.

small bags and pollen of the male plant is shaken over the blossoms. A plant undergoing artificial pollination is illustrated in figure 2.

Hop Yards for Experimental Testing

The experimental field at Corvallis, Oreg , consists of an area trellised and spaced like a commercial yard and another smaller section for growing seedlings for the first year's observations. The larger area, pictured in figure 3, is capable of accommodating about 3,500 plants spaced 8 feet apart. Included in this section are plantings of all domestic and available foreign varieties, together with seedling plants that appear worthy of growing beyond the first year. The smaller area, known as the seedling yard, is designed for growing first-year seedling plants for preliminary observation. Seedlings are planted 15 to 18 inches apart in the row and trained on strings attached to a wire approximately 6 feet from the ground level. About 3,000 plants may be grown under these conditions (fig. 4). Seedlings that appear to be of the types sought are then transplanted to the standard yard for further tests. Hop seeds may be sown in greenhouses or in coldframes in the field in early winter or early spring. In the growing season the

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Figure 4.—First-year hop seedlings in nursery yard. Note closeness of planting and variable growth.

Figure 5.—Seedling hops in greenhouse beds. The dome lamps may be used to supplement daylight during fall and winter months. Strong seedlings are thus developed for field planting in the early spring.

plants obtained are moved into the seedling yard or into field rows to be later included in the nursery. Seedlings growing in greenhouse beds are shown in figure 5.

Though, in general, growing conditions are kept favorable for plant growth in the experimental areas by following common commercial methods, the nature of the information sought requires certain widely divergent practices. One of these is the actual fostering of the development of the downy mildew disease by cultural practices favorable to its spread so that it will "run wild" among both the older plants and the seedlings under observation. Since resistance to this malady is one of the chief goals, its rapid spread is sought, to permit selection of resistant types. Where it may seem apparent that plants vary in reactions to insects, the latter pests may also be left uncontrolled. Since it is not desirable to select plants under soil conditions exceptionally favorable for growth, the use of fertilizers is restricted. Otherwise, plants are allowed to develop in a manner comparable to those in commercial yards.

Figure 6.—Experimental hop-drying chamber. The small cabinet within contains the samples of hops, placed in coarse mesh bags. The scale beam allows constant checking of moisture losses as the charge is dried. Drying temperature and heated-air flow may also be recorded.

During the growing season many types of observations are made. The development of downy mildew and the plant's reaction to it are recorded weekly for some 3,000 seedlings and foreign and domestic varieties. Data are also taken on infestations of aphids and red spider. Relative maturity, vigor, stem and leaf color, leafiness, abnormalities, and sex are also recorded in seasonal notes previous to harvest.

Late Clusters, Early Clusters, and Fuggles are grown in plots of sufficient size and number of plants to obtain information on yields. In 1934 and 1935 over 400 such plants were picked and weighed individually. Other less common varieties, such as Red Vine and Bavarian, are also grown though less extensively. Foreign strains and all promising seedlings are harvested individually but have not been grown on a comparative yield basis, for reasons indicated later. After picking, samples are dried in a small experimental drier (fig. 6) through cooperation with the Oregon station section of agricultural

engineering. The hops are then pressed into small bales resembling the commercial package except in size.

Chemical tests have been made on many samples to determine the soft-resin content as a means of obtaining some index of quality. Physical examinations have also been made for color, aroma, seed content, cone size and condition, and presence and appearance of lupulin. At present, the chemical and physical analysis of the dry hops is the ultimate test for brewing value. Actual brewing tests will be necessary to finally establish the suitability of new strains for commercial use

Breeding Objectives and Progress

In the hop-breeding project thus far, definite information has been obtained on a number of problems, and observations made since 1930, together with contacts with growers and dealers, have served to crystallize objectives.

Late Clusters, the dominant domestic sort, is normally a good yielder, has a high soft-resin content, and is otherwise well suited to brewing purposes. It is, however, quite susceptible to downy mildew, plant lice, and red spider. It is also leafy and late in maturity. Early Clusters is very susceptible to downy mildew and aside from being somewhat earlier is interchangeable commercially with Late Clusters The cones are larger and the vines a little less leafy. It is a favorite with pickers. Fuggles is resistant though not immune to downy mildew, usually making a fair crop when cluster varieties are severely injured Yields are decidedly lower than those of the Early Clusters and Late Clusters and the variety does not permit as much delay in harvest as does Late Clusters. It is also quite susceptible to red spider injury. The soft-resin content of Fuggles is usually below that of the cluster types and the commercial trade recognizes the variety as an individual class

Red Vine hops have been grown more extensively in earlier years than at present; very few uniform fields of this variety now exist. It is noted for its pleasing aroma and many growers believe a small amount of Red Vine hops adds in this respect to the quality of Late Clusters. The soft-resin content is comparable with that of Late Clusters. Chief objections to Red Vine are leafiness, many small hops—though the yield is good—late maturity, and susceptibility to aphis, which is due in part to profuse foliage.

Where suitable males are present, all of these varieties produce abundant seed, but the prevention of seeding might easily be accomplished by elimination of male plants. Inability to obtain satisfactory premiums for seedless hops has not encouraged growers on the Pacific coast to eliminate seeds.

None of 30 varietal strains introduced from other hop-growing countries has appeared to be superior or equal to those now grown on the Pacific coast. This may be comparable with the results of extensive corn trials in the United States where many varieties do well only within small areas or localities. Certain of the introduced varieties have made fair growth and several have exceeded Late Clusters in percentage of soft resins. In table 1 are given results of physical and chemical analyses of some foreign and domestic hops

TABLE 1.—*Physical and chemical analyses of hop varieties and seedlings grown at Corvallis, Oreg., 1935*

Variety or seedling	Color	Aroma	Lupulin	Cones	Total soft resin
Foreign varieties					*Percent*[1]
Landhopfen	Yellow green	Strong, pleasant	Yellow, very plentiful	Medium	20.88
Burgunder	Greenish golden yellow	Pleasant, flowery	do	Small	19.92
Bavarian[2]	Yellowish green	Mild pleasant	Lemon yellow, plentiful	do	19.17
Alsace	Pale green	Strong not pleasant	do	Medium	18.60
Golding	Greenish golden yellow	Mild, not pleasant	Yellow, plentiful	Small to medium	17.87
M 45	Yellowish green	Mild, pleasant	do	Medium	17.70
Spalter	Pale green	Excellent flowery	do	do	17.54
Elassar	Yellowish green	Very pleasant, flowery	do	do	17.54
Domestic varieties					
Late Clusters	do	Mild agreeable	Lemon, yellow very plentiful	Small to medium	19.12
Early Clusters	Golden green	Strong, pleasant	Yellow, plentiful	Medium to large	18.58
Fuggles	do	Mild, very pleasant	Lemon yellow plentiful	Medium	17.62
Red Vine	Golden yellow	Strong, not pleasant	Yellow plentiful	Large	17.11
Seedlings					
52-31	Pale green	Strong, pleasant	Lemon yellow, plentiful	Medium to large	19.71
8-12	Yellowish green	Mild, agreeable	Lemon yellow very plentiful	do	19.06
62-27	Pale green	Mild, pleasant	Yellow, plentiful	Small to medium	18.12
101-32	Bright green	Very mild, pleasant	Very plentiful	Medium to large	17.75
36-32	Pale green	Mild, pleasant	Plentiful	Small to medium	17.70
73-12	Yellowish green	Strong, unpleasant	Very plentiful	do	17.20
70-13	Pale green	Mild, pleasant	Yellow, plentiful	Medium	17.16

[1] Based on air-dry hops

[2] Of uncertain origin, possibly a domestic selection by growers

grown at Corvallis, Oreg., in 1935. Though the data are for 1 year only, the analyses are remarkably high.

The soft-resin content is based on individual determination of several resin components, which is the usual method of chemical analysis. The notes on physical characteristics of the various lots are of importance, since commercial dealers usually observe these points in trade samples Comparisons may be made between foreign and domestic varieties by reference to the table. Though all of the samples listed might be considered choice from a trade viewpoint, superiority of certain strains is indicated. In both 1934 and 1935 Landhopfen and Burgunder exceeded Late Clusters, the richest domestic variety, in percentage of soft resins. Analyses of certain of the better seedling selections indicate the possibilities for obtaining improved types in this important character.

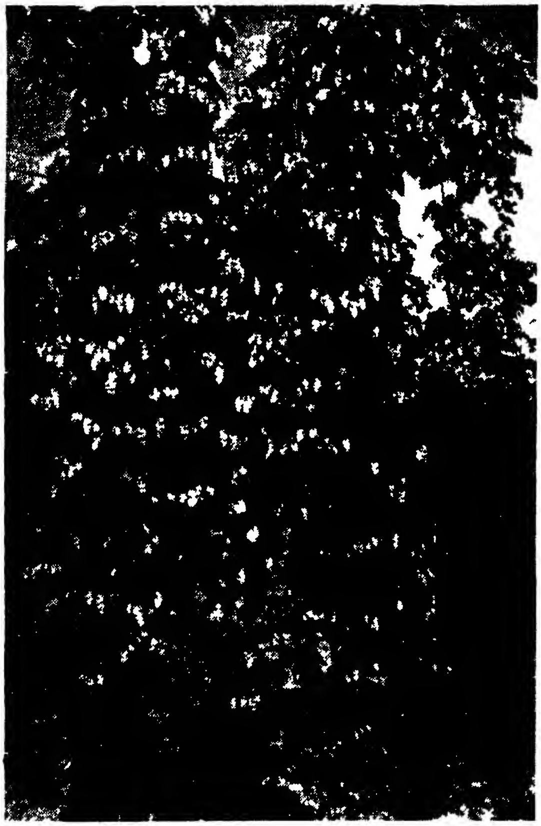

Figure 7.—A promising seedling hop plant having a cone type resembling Fuggles and leaves similar to those of Late Clusters.

Wide variations in physical traits may be noted, though soft-resin contents remain similar. Aroma particularly may vary from excellent to strong and unpleasant when other characters seem to vary but little.

Many seedlings have been grown at Corvallis since 1931. Seed has been obtained from domestic and foreign varieties from the experimental yard and from many commercial fields. These seedlings have been for the most part of inferior types. Many are male plants, others are dwarfed or otherwise undesirable, and only rarely is a plant producing "fair" hops obtained. One of the latter sorts, considerably better than usual, is illustrated in figure 7.

In the matter of soft-resin content, seedlings may vary over a wider range than varieties. In the 1933 season 29 of these varied from 9 to

17.9 percent,[7] while Late Clusters contained 17.9, and Fuggles 16.3 percent soft resins. In the crop of 1934 cones from 57 seedlings contained between 9.4 and 17.8 percent of soft resins. The percentage for Late Clusters was 17.8 and for Fuggles 14.8. Nineteen foreign varieties grown at Corvallis under similar conditions ranged from 14.2 to 19.4 percent soft resins. Similarly, the 1935 crop of 50 seedlings ranged from 11.1 to 19.7 percent; Late Clusters contained 19.1 and Fuggles 17.6 percent. Foreign varieties, 23 in number, varied from 14.1 to 20.9 in percentage of soft resins.

In aroma, many seedlings have compared to advantage with standard varieties while some are decidedly inferior.

Experience has demonstrated, both here and abroad, that plant reaction to downy mildew is difficult to ascertain. This is due to the irregularity of the occurrence and development of the disease. The nature of this problem may be indicated by the fact that one seedling of a very promising nature in the years 1931–33, free from mildew and of good agronomic appearance, mildewed severely in 1934 and 1935. Preliminary tests have shown that artificial inoculation of questionable plants by hypodermic injection of the mildew organism may be feasible. This would tend to supplement the work of nature in the development of the disease and make possible more rapid progress. Results at Corvallis offer some assurance of obtaining seedlings resistant to the downy mildew disease.

Since yields of foreign types have been obviously inferior to those of commercial varieties, comparative yield tests of the former with domestic sorts have not been made. Neither have any of the foreign varieties proved to be highly resistant to downy mildew.

Results thus far indicate that leaf, stem, cone form, and cone arrangement are fairly constant from year to year. Plants producing male or female or both types of flowers in any one year tend to be similar in other years though occasionally marked exceptions may occur.

Resistance to aphids and red spider has not been found in any varieties or seedlings observed. Though many plants have not been injured, several years' observation, as in the case of reaction to downy mildew, will be required to definitely determine the stability of this character.

In summary, of the improvements sought, agronomic characters, including high yield and desirable cone type, have proved to be the most difficult of attainment, judging from recent experience in the breeding project. Between 15,000 and 20,000 seedlings, of which approximately 3,000 have been grown to the cone-producing stage, have allowed selection of fewer than 10 with records of resistance to mildew, high resin content, and good agronomic qualities. Most of these may not survive continued tests.

It is proverbial among plant workers that varietal improvement usually requires consistent work over many years before great practical benefits can be shown. While propagation by cuttings simplifies the plant breeder's job in that plants "impure" from the hereditary standpoint may be reproduced as uniform, true-breeding commercial varieties, in the case of hops this advantage is counterbalanced by problems not usually met in such work.

[7] Based on moisture-free sample.

Large Numbers of Plants Needed for Effective Selection

Caring for large numbers of plants individually during a period of several years requires a large area and much labor. Picking and drying many samples separately and the making of chemical tests also present physical problems. All of these limitations mean that the work is necessarily slow.

Growers of the Pacific coast have shown new concern in improvement problems since 1931. Of interest in this regard also is the initiation of the varietal improvement project by the New York (State) Agricultural Experiment Station, previously mentioned.

Though European varieties have not to date proved to be adapted to conditions on the Pacific coast, the progress made in developing improved types in Europe by seedling selection offers hope for comparable progress in the United States.

Mildew Records

An obstacle common to all breeding for resistance to disease is the frequent necessity of waiting for natural development of epidemics before plant reaction can be obtained. Downy mildew appears capriciously, and 8 to 10 seasons may be required to adequately determine plant reaction to this disease. Yield and quality are variable characters requiring tests of several seasons' crops.

Methods of recording and comparing data on downy mildew reaction from season to season have presented a troublesome problem. At present such notes are taken at approximate weekly intervals while the epidemic is spreading, and plants are classified by numbers from 0 to 5 as representing progressively increasing numbers of leaves or branches infected by the disease. Comparative classifications of 2,827 plants upon which notes were taken in 1934 and 1935 are given in table 2. The differences of reaction from year to year due to variation in the development of the epidemic through the area are indicated. In 1934, for example, 294 plants were classified as no. 5 in reaction, or very susceptible. Of these, 183 failed to develop symptoms in 1935. Of the 1,788 plants classed as 0 in 1934, 1,543 did not mildew in 1935. The data show that even with downy mildew generally present, many susceptible plants may escape infection.

TABLE 2.—*Downy mildew, incidence in experimental yard, Corvallis, Oreg., 1934–35*

1935 classification [1]	Plants in each classification [1] in 1934						Total
	0	1	2	3	4	5	
0	1,543	99	304	58	62	183	2,249
1	41	2	7	3	6	10	69
2	165	8	92	22	20	60	367
3	2	0	2	4	2	2	12
4	1	0	2	1	0	1	5
5	36	3	25	15	8	38	125
Total	1,788	112	432	103	98	294	2,827

[1] 0 to 5 represents progressively increasing numbers of infected leaves or branches.

Seasonal Productivity

Various agronomic reasons for unproductive hills were suggested by Bressman (*1*), and Stockberger (*19*) indicated certain conditions influencing yields. Attempts have been made to determine the consistency of yield of hop plants (*18*) from year to year. Growers often experience unexplainable irregularity of development and production in yards usually uniform. The question has arisen also as to the possibility of continuously selecting from the most vigorous plants as a means of increasing yield by isolation of more vigorous types. Information is being sought that will answer these questions more completely.

In 1934 and 1935 hill surveys were made of 25 different marked areas of 100 hills each in some 15 yards, on several soil types in western Oregon. Plants were classed as S (strong), M (medium), W (weak), X (untrained—also a weak type) and O (indicating no plant present), at two periods in each season. A contingency table (table 3) shows the relations between 1934 and 1935 notes taken just previous to harvest. Hills designated as O in 1934 were replanted in the early spring of 1935. The data indicate unexpected irregularity in the seasonal growth and productivity of any particular class of plants. Frequently individuals classified as strong in one season may be considered as weak or even fail to produce hops the succeeding year. Continuation of records may provide information serving to throw light on such variations

TABLE 3.—*Summary comparing hill survey of plant types, commercial yards, Willamette Valley, Oreg., 1934–35*

1935 classification [1]	Plants in each classification in 1934					Total
	S	M	W	X	O	
S	390	51	216	21	95	773
M	165	4	98	9	60	336
W	85	1	91	33	227	437
X	10	0	9	6	29	54
O	45	0	27	5	51	128
Total	695	56	441	74	402	1 728

[1] S=strong, M=medium W=weak X=untrained O=no plant present

Production data add more precisely to the interpretation of this problem. Actual yields on individual plants from the experimental yard in 1934 and 1935 are available on the Late Clusters, Early Clusters, and Fuggles varieties. Correlations between yields of the two seasons are indicated in table 4.

TABLE 4.—*Yield data for three varieties of hops, 1934–35*

Variety	Plants	Mean yield		r value	P value exceeds—
		1934	1935		
	Number				
Late Clusters	104	7.9±0 50	12 14±0 49	0 19	0 05
Early Clusters	113	7.19± 40	7 94± 31	57	.01
Fuggles	125	5 60± 20	7 26± 19	.39	.01

In general a significant relation between yields from year to year is exhibited, although the correlation coefficient for Late Clusters is marginal.

Other Important Technical Studies

Analyses of the results of artificial pollination have been complicated by two major problems—(1) the slow and irregular germination of hop seeds, and (2) the doubtful results of bagging. Somewhat detailed studies have shown greatly increased and more rapid germination as a result of cold treatments. One of the best of the treatments used was placing the seeds in moist blotters in a germinator for 5 days at room temperature followed by refrigeration for 5 weeks at 5° C. Such procedure has increased germination from less than 10 to over 70 percent. Once seeds have germinated and plants have emerged, growth may be rapid. Artificial illumination has been reported by Bressman (*2*) as of value in stimulating vegetative development.

Results of bagging and subsequent pollinations have been inconclusive. Some seeds have developed within and outside of glassine and parchment bags whether or not enclosed flowers were artificially pollinated. The bags used have been tightly secured to the branches by paper clips. Flowers have been covered at various early stages of development, from the period immediately preceding the appearance of the stigmas through the time when they withered. Whether plants form seed parthenogenically, without fertilization, or whether seed obtained from bagged, unpollinated flowers will grow has not been satisfactorily determined. Thus far the possibility of incomplete exclusion of pollen from bagged flowers does not seem adequate to explain the results obtained. Winge (*20*), Howard (*5*), and others, however, have reported the failure of seeds to set when pollen was not allowed to reach bagged flowers. Relations between ability of male pollen from different plants to cause fertilization and ability of females to produce seed are also being determined. Until seed formation and germination can be more accurately controlled, the results and the value of hybridization will be uncertain.

Constancy in development among various plant characters from year to year is indicated in table 5. Fundamental information is needed in this respect to form a basis for plant selection.

TABLE 5.—*Constancy of plant vegetative characters*

1935 classification	Plants in each classification in 1934						
	Dwarfs	Dwarfed	Witches'-broom	Ragged	Russeted	Colored vines	Total
Dwarfs	2	0	0	0	0	1	3
Dwarfed	13	6	1	1	2	1	24
Witches'-broom	0	0	17	0	0	0	17
Ragged	19	17	3	65	18	66	188
Russeted	4	3	0	5	29	14	55
Colored vines	6	14	0	4	4	265	293
Total	44	40	21	75	53	347	580

Descriptive differentiation of the classifications seems unnecessary to illustrate the variations in vigor and type of growth from season to season. With the exception of colored vines, other classes are plant

weaknesses and therefore undesirable. Occasionally vigorous plants of good general type may show light russeting of leaves. Ragged plants develop torn or ragged leaves and flowering branches may be partially or entirely sterile. The type known as "witches'-broom" is apparently the sterile dwarf described by Salmon (*7*). It is possible that some of the conditions listed may be pathological while others may be due in part to genetic factors. While detailed notes are available for 2 years only, a marked constancy of growth character is evident in certain groups.

In dioecious species such as hops the expression of sex is of particular interest. Development of hop plants as to sex appears to be generally constant though infrequent, wide deviations apparently occur. It is a fairly common observation of growers that in some years more male plants appear than usual.

In approximately 1,200 seedling plants in the experimental yard upon which notes have been taken for sex, the following deviations occurred in 2 years, 1934 and 1935:

	Plants
Change from male to female	5
Change from male to hermaphrodite [8]	2
Change from female to male	1
Change from female to hermaphrodite	1
Change from hermaphrodite to male	2
Change from hermaphrodite to female	5

[8] See footnote 7, p. 1230.

Deviations may be noted in all degrees of sexual expression. Data are insufficient to justify generalizations as to which transformations occur most frequently or to suggest possible explanations. Observations of Chartschenko (*3*) in this respect are noted later. Salmon (*7*) has recorded relative frequencies of male and female individuals in seedling progenies, as well as other developmental types.

The variation to be expected in resin analysis of hops from the same plants from year to year is a factor requiring careful study. Even though individuals are harvested at as nearly the optimum time as possible and all other factors are controlled similarly, large differences may exist from season to season. This is illustrated in table 6, comparing examples taken at random from yearly analyses of individual plants.

TABLE 6.—*Soft-resin contents of hops from individual seedling plants*

Seedling no.	Soft-resin content for— [1]			Seedling no.	Soft-resin content for— [1]		
	1933	1934	1935		1933	1934	1935
	Percent	*Percent*	*Percent*		*Percent*	*Percent*	*Percent*
36-7	18.22	17.95	16 03	62-27	17.53	14.93	18.12
52-10	17.10	16.96	15.93	8-10	18.70	17.61	16.77
19-33	17.49	16.77	14 36	56-28	14.60	10.24	12.88

[1] Percentages on dry basis.

The data show the relative inaccuracy of analysis of a single year's crop as a strict indication of plant behavior, at least for some individuals. Plants might, however, be placed in general groups as good, fair, and poor, with reasonable accuracy in most instances. Increased

experience and additional care in harvesting, drying, and packaging of samples will undoubtedly decrease the errors encountered.

Contributions by Various Investigators

A brief review of investigated points of interest in hop breeding will indicate the nature of some of the problems and the facts obtained in other hop-growing countries. Though hops were investigated at an early date, comparatively little information on breeding aspects may be found in the literature. Reference has already been made to certain work. An attempt to bring together scattered supplementary facts and further outline the general background seems desirable.

It was early noted that plants from seeds were variable and most often poor (*13*). A wide range of maturity was also noted in such progenies (*15*). In addition it was recognized that new varieties might arise either from seeds or from bud variations.

Salmon (*7*) obtained the following results from seed progenies derived from controlled pollinations:

From 256 seeds 87 seedlings were produced, of which 52 plants were normal and 35 were sterile dwarfs.

From 285 seeds 67 seedlings included 66 fertile and 1 dwarf plant.

From 261 seeds 120 plants, all of normal vegetative growth, included 108 females, 111 males, and 1 hermaphrodite.

From 899 seeds 109 seedlings included 79 normal plants and 30 sterile dwarfs.

The dwarf plants made little growth compared to normal plants and failed to form flowers of any kind. Such results represent the expected appearance of many inferior plants in seed progenies, however derived. Studies of three groups of seedlings reported by Fruwirth (*4*) indicated the proportions of female plants to be 66, 77.7, and 90 percent respectively, in the progenies considered.

Pollinated cones were found by Winge (*20*) to be larger and heavier than those whose flowers were not pollinated. Unpollinated hops were observed to remain longer in the bur, and stigmas at the stem end were noted to appear first (*5*). Fertilized cones were also thought to mature earlier and resist mold to a greater degree than those unfertilized.

In order that pollination might be complete, it was recognized that male plants must shed pollen throughout the bur period of the females. Pollen from hermaphroditic plants was determined to be viable and to be capable of fertilization (*20*). Chartschenko (*3*) reported female flowers of such plants to produce viable seed.

The impossibility of crossing two female plants has been pointed out, though combinations of female varietal characters in one individual may often be desirable. In addition it seems obvious that since male plants do not bear hops, their value in use as parents must be determined with appreciable difficulty.

As early as 1894 Stambach, cited by Fruwirth (*4*), planted out seedling hops for observation. Remy, mentioned by the same writer, studied resins and tannins of seedling hops in 1898. He crossed cultivated female varieties with wild males, crossed an F_1, or first generation, male of the progeny with a cultivated female plant, and then recrossed an F_1 male of the latter progeny back to a cultivated female. This is a comparatively complicated crossing scheme but is occasionally used by plant breeders.

Reversals in the nature of the sexual character of hop plants have been reported by several workers, according to Fruwirth (*4*). Chartschenko (*3*) has given examples of sexual changes. A male plant was described as changing to a normal female in 2 years, being a hermaphrodite in the third, and a normal male again in the fourth year. In another case a cutting from a female plant produced a vine bearing male flowers. In yet another instance two female plants changed to hermaphrodites. Vegetative increase of these also gave rise to hermaphrodites.

Much interest has been shown in studying relations of numerous plant characters to the important property of resin content and other indications of quality. Fruwirth (*4*) reported high yield to be associated with inferior aroma, greater foliage production, stouter strigs (center stem of cone), and plant longevity. Chodounski, mentioned by Fruwirth, thought coarser hops to be characterized by inferior hairing, lack of uniformity in strength, abnormal structure, and other characters of the strig. Sutora, cited by the same writer, concluded that a coarser strig and darker green color of the hop is associated with a lower tannin content. According to Fruwirth, finer hops were thought by Wagner to have smaller bracts and a smaller bract area. Percival (*6*) pointed out that delicacy and weakness of cones were often met with in hops of the best quality. Salmon has indicated that a theoretically choice English hop might combine high soft-resin content with the aroma of present English or Saaz varieties (*8*). He stated that total resin contents remain fairly constant from season to season in varieties generally (*9*). Chartschenko (*3*) reported that Russian work had failed to establish any female characters as being associated with resin content. Within varieties no significant relation was found between resin content and yield of green hops or earliness of ripening, or in most cases between earliness and yield of green hops. Appreciable variation was found as to resin contents between vegetative selections within varieties. Results of analyses of male plants in which resin contents varied from 1.77 to 3.48 percent were given. Attention was directed to the importance of this in view of the fact that the male contributes half the inheritance of the progeny in this and other characters.

It has been accepted that variety has more to do with resin and oil content of hops than soil or locality. Other factors that influence these characters are climate, fertilizers, maturity, drying methods, and seed content. The aroma of certain types of American hops has been compared with the odor of turpentine, black currant leaves, onions, rue, and apples, and therefore said to be inferior to that of European hops (*8*). Resin content (*14*) and aroma (*16*) have been found to be inherited traits and progeny plants may exceed the female parent in these important attributes.

In one instance of a cross, the aroma of an Oregon female plant was exhibited by about three-fourths of its progeny. Aroma has been shown to be transmitted through the male, by the same investigator (*16*).

Characters recognized as constituting differences among varieties have included vine color and length of internodes; maturity, arrangement, and form of strobiles; color, number, and form of leaves; leafi-

ness in proportion to cones and stems; and relative dry weights of the cones. Though variation seemed less marked in males, they were found to be generally as variable as female plants (*22*).

American varieties introduced into England have proved to be unsuited there and it has been concluded (*8*) that introduction of foreign varieties has little value except for use as parents in obtaining superior seedlings. This may represent the major value of varietal introductions made into the United States.

Since the appearance of downy mildew in European hop culture, attention has been directed to varietal response to this and other diseases. Salmon (*9*) has reported many of these results, which eventually have served to classify all varieties as mildew-susceptible though in varying degrees. Saaz hops, at first thought to be immune, mildewed in 1932. Fuggles is one of the most resistant types, but both leaf and cone infection have occurred. Some strains may be resistant to cone infection. Many of the most resistant sorts are now in commercial use. Salmon (*10*) has also observed certain varieties and seedlings to be resistant to blue mold.

In England the "mosaic disease", so called because of its mottled coloring effects on the leaves, affects all hops except the varieties Fuggles, Tolhurst, and Colgate. Nettlehead and chlorotic diseases have been found only on Fuggles (*8*). In 1926 mosaic disease was serious in Yugoslavia. Mosaic disease, nettlehead, and the chlorotic diseases are virus [9] troubles not generally reported from hop-growing countries.

Crossing experiments with hops have been carried out in most European countries since 1900 Hybrids between *Humulus neomexicanus* and *H lupulus* have been reported (*11*). Imperfectly formed seeds of *H lupulus* and *H japonicus* have been obtained (*20*), but these have failed to produce plants

Cytologic investigation has received little attention to the present time, though Winge (*20*, *21*) has studied the genus *Humulus* in some detail. Chromosome numbers in *H. lupulus* have been found to be 20 in the vegetative cells (diploid). These have been designated as 18+2X in the female and 18+X+Y in the male. In *H. japonicus* 17 have been assigned to the male (14+3X) and 16 to the female (14+2X) (*21*)

Absence of more complete information on inheritance of plant characters is undoubtedly due to the sexual nature of the hop species and attendant problems in obtaining satisfactory progeny tests. As previously mentioned, the situation approaches that in higher animals.

Breeding Program Slow But Promising

Isolation of improved varieties of hops resistant to downy mildew and otherwise superior to present domestic sorts appears to be reasonably practical. Present objectives in hop breeding are well recognized and methods of reaching desirable ends are in the process of establishment. Results obtained in England indicate promise for consistent investigation. Hop breeding experiments initiated at Wye, Kent, in 1907 have resulted in significant improvements of the English crop. Salmon (*12*) has recently announced the development of two valuable

[9] An infectious principle not recognized as due to a particular organism, but capable of causing disease.

new varieties, Brewer's Favourite and Brewer's Gold. The first of these is a seedling originating in 1909 from a plant of Oregon Cluster (probably Late Clusters) introduced into England, and it has been tested extensively since that time. Brewer's Gold is also a seedling, first raised in 1919. These varieties are high yielders, producing cones rich in soft resins and otherwise acceptable to both brewer and grower.

Based upon breeding investigations with crops of other kinds as well as hops, continued experimentation will be necessary if progress is made such as has been reported in other countries. The breeding project requires observation of numerous plants in comparative field and chemical tests over a long period.

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APPENDIX

WORKERS AND STATIONS CONCERNED WITH VARIETAL IMPROVEMENT IN HOPS AND HOP BREEDING [11]

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[11] No implication is made that this list is complete, since it is based in the main on correspondence with foreign workers.

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IMPROVEMENT OF FOREST TREES

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FORESTRY is a young profession. In comparison to agriculture, it has just been born. Under pressure of necessity, farmers were breeding crop plants long before genetics supplied the key to many of the mysteries they encountered; but the natural products of the forest were plentiful and were taken as needed, without thought of artificial replacement Until very recently, indeed, even foresters have been

Figure 1.—A "man-made forest" of slash pine in southeastern Louisiana. The artificial regeneration of cut-over lands on such a large scale emphasizes the need for guidance from sound genetics work in the improvement of forest trees.

content to utilize wild trees as they were found. This lack of interest in the improvement of forest trees has been due both to the lower unit value of the stock and to the greater difficulties involved in breeding work.

Various factors have been responsible for a gradual change in attitude within recent years. The rapid recession of the timber supply accessible to established wood-using industries; the inferior quality

of much of the second-growth wood; more stringent quality requirements in the finished product to meet the competition of other manufacturers or of substitute products, necessitating uniformity or improvement in quality of the raw wood material; the denudation of forest areas by uncontrolled commercial exploitation and the necessity for having them restocked and managed by public agencies in the public interest (fig. 1); the urgency of soil conservation on nonagricultural lands—all these have played a part in exerting pressure for a more intelligent attitude toward the forest problem as a whole, and the exploration of any possibilities that might be promising.

The tree breeder, then, has just begun to roll up his sleeves. In comparison with his confreres who deal with the older agricultural crops, his attitude is one of humility; he is only at the beginning and he has much to learn. But on the other hand, because his work is all before him, he sees infinite possibilities ahead for the improvement of forest trees by breeding and selection.

This should be kept in mind by the reader as he peruses the following brief account of the present status of breeding work with forest trees. In various parts of the world, considerable necessary spadework has been and is being done. Much of it might not be called either genetics or breeding by those who have become facile in dealing with the smaller, quicker maturing crop plants. Nevertheless, this spadework will be of great value to forest-tree improvement, and it is essential to the building up of a science of forest genetics. The appendix gives a concise summary of most of the work relating to forest-

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UNTIL *very recently, foresters have been content to utilize wild trees as they were found. There has been a gradual change in viewpoint, brought about by the same factors that have exerted pressure for a more intelligent attitude on the part of the public toward the forest problem as a whole—the depletion of the timber supply accessible to established wood-working industries; the inferior quality of much of the second-growth wood; more stringent quality requirements in the finished product; the denudation of forest areas by uncontrolled commercial exploitation; the urgency of soil conservation on nonagricultural land. Today foresters are eager to explore any possibilities that might be promising, and tree breeding seems to be one of the most promising. In comparison with the breeder of the older agricultural crops, the tree breeder has just begun; his attitude is one of humility; but because his work is all before him, he sees infinite possibilities ahead. In various parts of the world much necessary spadework is now being done to lay the foundations of a true science of forest genetics.*

tree breeding now being carried on by public and private agencies in the United States, and some of the work being done in foreign countries.

The improvement of any wild stock should logically begin with (1) a segregation of varieties, races, and strains of the wild population. It should then proceed to (2) the evaluation of the characteristics of each group, (3) the selection of the best individuals in each of the best strains, (4) breeding and selection, which controls both parents and utilizes the best germ plasm available in these wild stocks, and, finally, (5) the production of decidedly new types by hybridization and by advantageous use of induced or natural changes in the normal number of chromosomes (polyploidy). The improvement of forest trees strictly along these lines would require extensive investigation and planting over many years. Fortunately, all five phases can well be carried on simultaneously.

STUDIES OF SEED ORIGIN—SPECIES, VARIETIES, RACES, STRAINS

For more than 60 years investigators have recognized the importance of seed origin, for which the term "provenience," meaning origin, is often used. The importance of races and strains of forest species first became apparent in Europe, where artificial regeneration of forest stands has been in progress for a much longer period than in the United States. European foresters began to realize that constant and important variations appeared between progenies from seed obtained in different regions. For example, in Sweden, Scotch pine grown from European seed often produced trees of very inferior forest form. Careful study indicated that proper selection of the seed source was necessary for the production of a desirable type of growth and an economically profitable stand. These investigations have led to fairly well controlled seed certification in some parts of Europe.

Forest research stations in the United States (fig. 2) have also been interested in this problem of seed origin (fig. 3) and experimental plantations were started over 20 years ago at several western stations. Test plots established at the Pacific Northwest Forest Experiment Station in 1915, with seed of Douglas fir, have already given valuable data on the existence and characteristics of various strains within this species. Seven apparently superior strains of ponderosa pine have been segregated at the Northern Rocky Mountain Forest Experiment Station from test plots established 23 to 27 years ago. Work at these and other stations is described in the appendix.

The establishment of the Eddy Tree Breeding Station (now the Institute of Forest Genetics, California Forest and Range Experiment Station)[1] in 1925 initiated a project for the intensive study of various problems in forest genetics. Extensive tests at the institute include 100 species and named varieties of pine (the genus *Pinus*) and innumerable climatic forms of many of these species. The seed has

[1] The Eddy Tree Breeding Station was originally founded and financed by James G Eddy at Placerville, Calif. In 1931, the station was incorporated and deeded to a board of trustees, the name being changed to the Institute of Forest Genetics Between the years 1931 and 1935 the institute received aid from the Carnegie Institution and the U. S Department of Agriculture (Bureau of Plant Industry, Soil Conservation Service, and Forest Service) On July 1, 1935, Congress granted funds to carry on work in forest genetics at the California Station and in this year the property of the institute was deeded to the Federal Government and became part of the California Forest and Range Experiment Station.

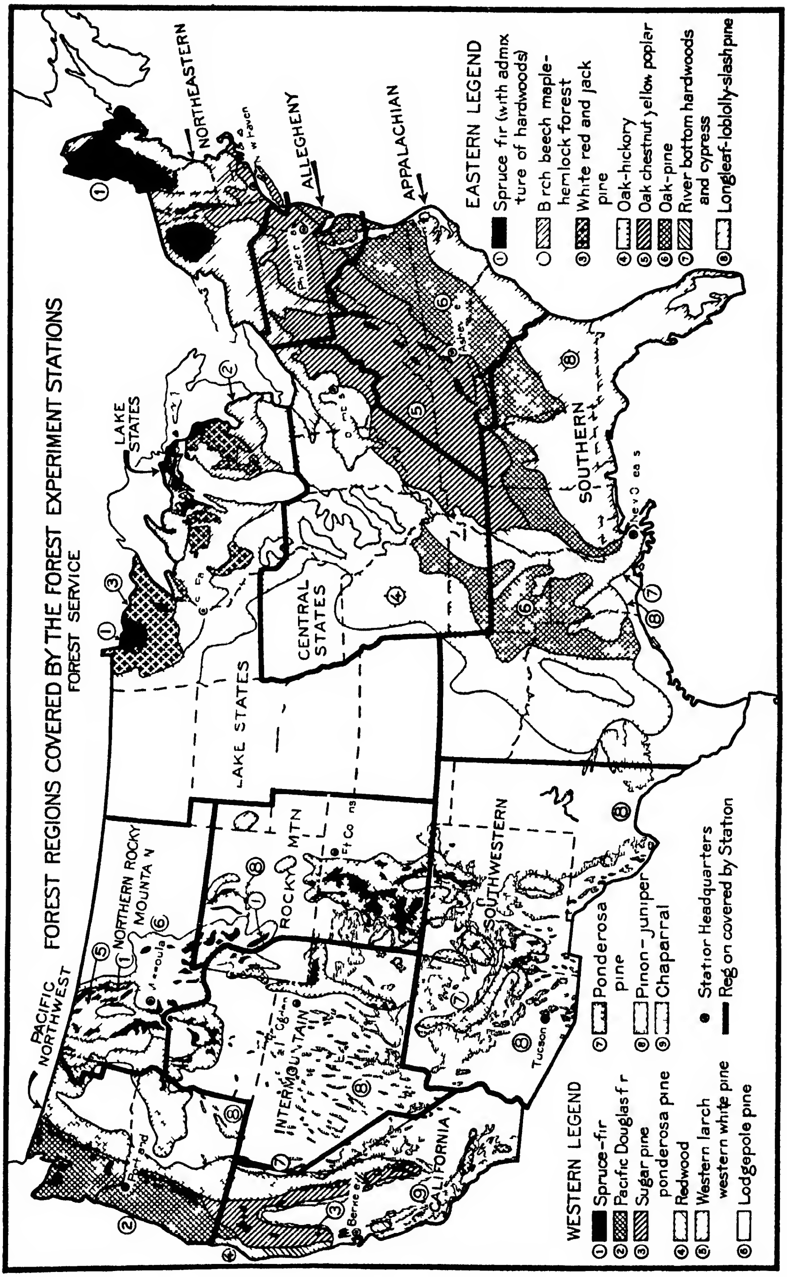

Figure 2.—Regions covered by the forest experiment stations of the Forest Service and the principal timber types of the regions.

been obtained from approximately 40 countries. In addition to the work with *Pinus*, 35 species of conifers, representing 17 genera, and 20 species of hardwood trees, representing 13 genera, have been included in this project, which at the present time is apparently the most comprehensive program of this nature in the United States. Valuable data have already been collected from these plantations,

Figure 3.—The importance of seed origin is shown by these 5-year-old Scotch pines. The tree on the left, of central European origin, has inherited rapid growth but a very poor and ultimately unprofitable growth habit. That on the right, from seed collected in Norway, has grown more slowly but will develop into a good forest tree.

and the institute will undoubtedly evaluate superior germ plasm for the breeding and selection of superior forest stocks.

Briefly stated, the investigations in connection with the problem of seed origin have shown that in many, if not all, important forest species there are rather distinct races and strains that differ in their hereditary response to a given complex of environmental conditions. Such races and strains probably have been evolved in response to the environment peculiar to their original habitat. Although the best reforestation results in any particular region can usually be expected from seed collected locally, or from a region in which the seed trees have been subjected to apparently similar environmental conditions, there are enough exceptions to this generalization to indicate that a great deal more investigation is required before the inherent adaptability of races and strains can be accurately cataloged.

INDIVIDUAL SEED-TREE PROGENY TESTS

Individual seed-tree progeny tests resulted from the realization that seed origin was of tremendous importance to the forester in considering

artificial reforestation. Observations that the individuals of the same seed origin showed marked differences in growth habit, in rate of growth, and in resistance to disease, climate, and site conditions, stimulated a further refinement in seed-selection studies. Investigations were soon started on the inherent characteristics of the progeny of individual

Figure 1. – Individuals of ponderosa pine growing in the same stands show inherent differences in vigor of growth. These two 7-year-old trees are from wind-pollinated seed collected from different seed trees in the same field plot in Eldorado County, Calif. The sister seedlings of both these trees were uniformly more vigorous than those of the slower growing pine of figure 5.

trees. Recognition of only the female parent was involved, since most of the important forest trees are wind-pollinated, and the source of the pollen that had fertilized the seed was necessarily unknown.

A number of European institutions are now engaged in individual seed-tree progeny tests. Oppermann, in Denmark, was among the first to insist on the necessity of carefully selected seed trees. Nicolai of Danzig, in particular, has stressed the importance of this problem and has started work with several forest species.

In the United States, many of the forest experiment stations have included individual seed-tree progeny tests in their research program. The Rocky Mountain Station has located individual trees of the ponderosa pine which are apparently mistletoe-resistant and has begun individual progeny tests with seed from these trees. Mistletoe infection often seriously retards the growth rate in this region and on the poorer sites often results in high mortality. Individual seed-tree progeny tests with green ash at the Lake States Station indicate that there are inherently different climatic races within this species.

An extensive progeny test was started in 1929 at the Institute of Forest Genetics with 742 individual seed trees of *Pinus ponderosa* (ponderosa pine) and its varieties *scopulorum* and *jeffreyi* (Jeffrey pine) Results to date indicate that there are apparently innumerable local strains, each with distinct morphological and physiological characteristics, and that individual trees vary strikingly in their ability to produce superior seedlings (fig. 4). This test included seed trees from 60 counties in 12 Western States and British Columbia (fig. 5). A more intensive progeny study, restricted to Eldorao County, Calif., where types with the greatest hereditary vigor seemed to occur, was started with the 1934 seed crop. The institute is also testing the individual seed progenies of 16 species and natural hybrids of walnut.

Figure 5.—This tree is typical of the comparatively slow growth of the British Columbia strain of ponderosa pine. Compare it with the more vigorous trees of the same age shown in figure 4. Racial differences are clearly indicated.

The results obtained from individual seed-tree progeny tests indicate that individual trees, growing under the same environmental conditions, vary greatly in their ability to produce good offspring and that it is therefore necessary to establish criteria for the recognition of heritable qualities. Adequate information for the description of good seed trees is not available at present.[2]

HYBRIDIZATION OF FOREST TREES

Numerous natural hybrids have been observed from time to time and the parentage of some of these has probably been accurately ascertained. Among such natural hybrids the following may be noted:

Larix eurolepis[3] (Dunkeld larch) from *L. europaea* × *L. leptolepis*
L. gmelini × *L. Kaempferi.*
Pinus sondereggii from *P. palustris* (longleaf pine) × *P. taeda* (loblolly pine).
P. halepensis × *P. pinaster.*
P. nigra × *P. sylvestris.*
P. montana × *P. sylvestris.*
P. montana × *P. nigra.*
Picea sitchensis × *P. canadensis.*
P. engelmannii × *P. canadensis.*
Salix coerula (cricketbat willow) from *S. alba* × *S. gracilis.*
Ulmus glabra × *U. montana* (Huntingdon elm).
Quercus cerris × *Q. suber* (Lucombe oak).
Royal walnut hybrids (eastern black walnut × various California black walnuts).
Poplar hybrids (Eugenei poplar, Serotina poplar, and others).

[2] Additional information on individual seed-tree progeny tests is included in the appendix.
[3] Species names have too often been applied to hybrids between tree species; in the case of poplars, to hybrid clones existing as a single sex. Hybrids are not species and naming them as such can only lead to confusion.

Many of these hybrids grow more vigorously than either of their parents, and in some instances other valuable properties or characteristics have been noted. For example, the Dunkeld larch is said to be resistant to the larch canker, and the wood of the cricketbat willow is said to be particularly well adapted to the manufacture of cricket bats.

Early Work

If possible, tree breeding should begin with stock that has been selected on the basis of its breeding quality (superior germ plasm), but since 1845 investigators have been interested in the possibilities of hybrids between species of forest trees, primarily because of the fact that species hybrids often surpass their parents in vigor of growth (so-called hybrid vigor). Klotzsch[4] is generally considered to have produced the first artificial hybrids between forest-tree species. In 1845 he hybridized two species each of pine, oak, elm, and alder, and observed that the resulting hybrids possessed growth characteristics superior to their respective parents.

Sporadic attempts to hybridize forest-tree species continued over many years. Ness, working at the Texas Agricultural College, produced a few hybrids between the live oak and the overcup oak in 1909, and a limited amount of breeding appears to have been continued at this station. Henry, working in England, produced several fast-growing poplar hybrids and in 1916 published a paper on the possibilities of obtaining rapid-growing forest stock by hybridization. Since 1916, there have been a number of publications discussing various aspects of the possibilities of hybridizing trees. The loss of our native chestnut through the introduction of the Asiatic chestnut blight stimulated interest in breeding this group, and as a result W. Van Fleet, of the United States Department of Agriculture, carried on breeding work with American and Asiatic chestnut species in an effort to produce an immune or resistant timber type.

Recent Work

The chestnut-breeding work started by Van Fleet has been continued and expanded by the Division of Forest Pathology, Bureau of Plant Industry. Selections have been made from the most promising forest strains of the Chinese hairy chestnut, *Castanea mollissima*, and of forest types of the Japanese chestnut *C. crenata*. First-generation hybrids between Asiatic and American species are usually remarkable in vigor, ordinarily excelling all other hybrids in this respect. Selective breeding has also been directed toward the development of small-sized nuts useful in mast production on trees that might be grown in soils not well adapted to either orchard or forest planting.

The first comprehensive project in hybridization within a tree genus was started in 1924 by the Oxford Paper Co., Rumford, Maine, in cooperation with the New York Botanical Garden, New York, N. Y. The primary purpose of this work was to produce new poplars valuable for pulpwood reforestation (fig. 6). This work has been highly successful. A total of about 13,000 hybrid seedlings was obtained from about 100 different cross combinations between 34 different

[4] See Bibliography, published in the Yearbook separate of this article.

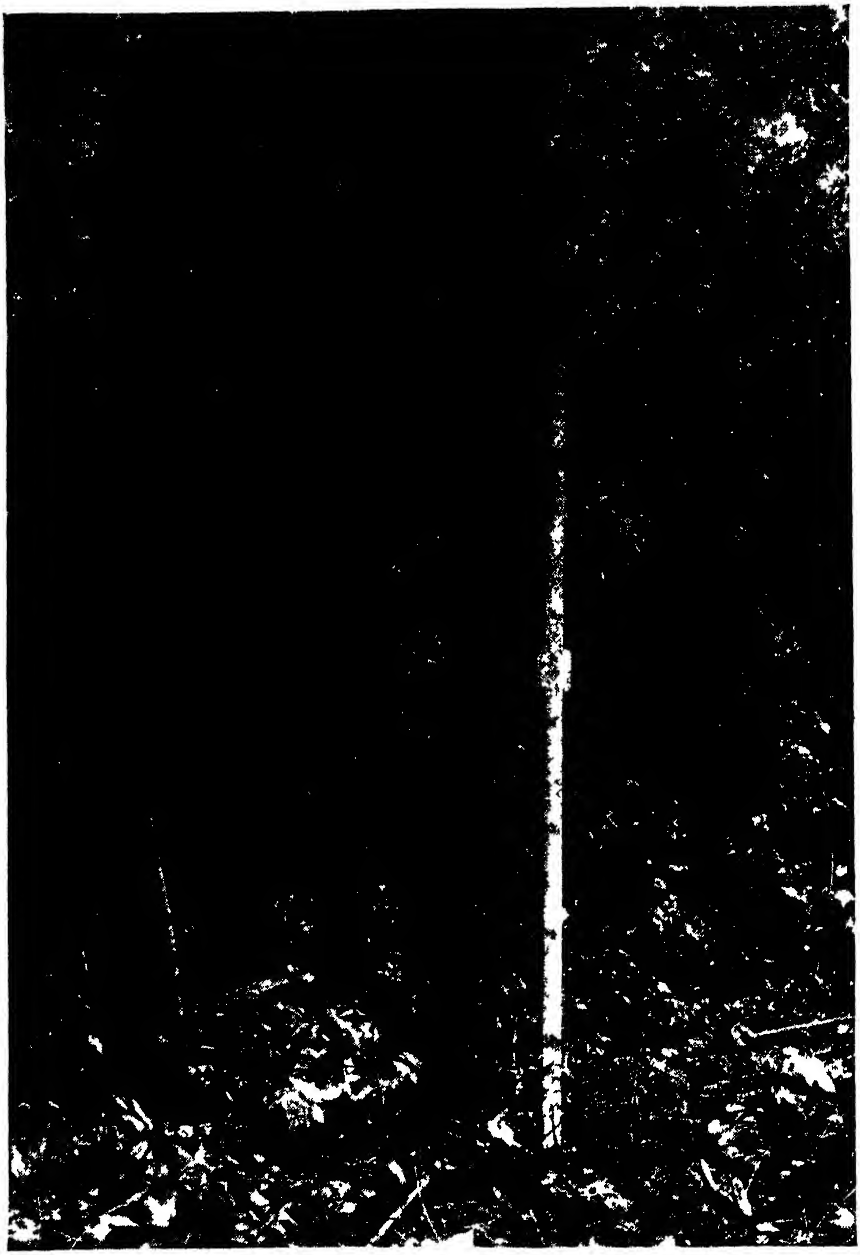

Figure 5.—The Strathglass poplar, one of the selected hybrid poplars produced by the Oxford Paper Co., after 7 years of growth in the field. This tree is approximately 7 inches in diameter and 37 feet tall. It is rather heavily branched, but the branches are small and should offer no difficulties to the use of the wood for soda pulp.

species, varieties, and hybrids of poplars. The parents included 3 white poplars, 5 aspens, 17 black poplars and cottonwoods, and 9 balsam poplars or hybrids belonging in this group. Many of the new hybrids appear especially promising because they surpass the older hybrids, at least during the first 8 years of their life, in rate of growth, resistance to disease and climatic conditions, and habit of growth (fig. 7).

Figure 7.—That well-directed breeding can produce trees immune or highly resistant to tree diseases is demonstrated by these two poplar hybrids. The picture was taken in early September. The trees at the right, without leaves, are members of a clone which is highly susceptible to *Melampsora* rust disease. The trees at the left, in full leaf, are members of a hybrid clone that is much more resistant to this disease. These hybrids are the same age and have the same female parent but different male parents.

Breeding work was undertaken at the Institute of Forest Genetics in 1925 and the institute has now approximately 60 hybrid seedlings involving 8 pine species and varieties as parents.

In 1930 the Brooklyn Botanic Garden, Brooklyn, N. Y., initiated a project for the breeding of chestnut, to produce hybrids that would combine good forest form with immunity to the chestnut blight. Some of the hybrids that have been produced give promise of excellent timber form and resistance to the disease.

The most recent large-scale breeding work was undertaken by the tree crop unit of the Forestry Division, Tennessee Valley Authority, Knoxville, Tenn., to develop trees that will combine good timber qualities with the production of annual crops of fruit (nuts, acorns, berries) of high quality and quantity. Such trees are to be used in tree-crop plantings, where the fruits will produce an annual income and the mature trees can be harvested for lumber or chemical wood.

The work of the Tennessee Valley Authority is of special interest because it aims at an annual income for the forest or wood-lot owner. For example, a stand of oak that will produce a large quantity of acorns will probably more than pay its way to maturity by the hog feed they provide, and if this production can be combined with excellent timber quality, forest planting to prevent soil erosion will

Figure 8.—Artificial hybrids between longleaf and slash pines produced at the Southern Forest Experiment Station show wide variation in susceptibility to brown spot (a needle disease of longleaf pine) in the same plantation: *A*, A 3-year-old hybrid seedling, highly susceptible to brown spot, has lost all of its older needles; *B*, another hybrid of the same age, is relatively free from the disease and shows superior growth and vigor.

be profitable to many southern hill-farmers. Improvement of our best annual-crop trees by hybridization and selective breeding will be essential to the successful and profitable combination of tree crops and forestry on marginal and nonagricultural farm lands.

At the present time the Northeastern Forest Experiment Station, New Haven, Conn., is starting a project in forest genetics directed toward the improvement of forest trees in the Northeastern region. It is expected that the program will include practical and fundamental research on seed origin, progeny tests, selective breeding, and hybridization.

Numerous other investigators in recent years have hybridized species of forest trees to a limited extent. At the Southern Forest Experiment Station, New Orleans, La., hybrid seedlings of *Pinus palustris* × *P. caribaea* (longleaf and slash pines) were obtained in 1929 (fig. 8), and also hybrids between *P. sondereggeri* (itself a hybrid)

and *P. palustris* and *P. taeda*, respectively. Workers at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo., have successfully crossed individuals of a strain of ponderosa pine that is apparently immune to mistletoe. At the Petawawa Forest Experiment station, Petawawa, Ontario, Canada, red spruce and Norway spruce were successfully hybridized in 1932, and in 1936 *Populus canescens* was crossed with *P. tremuloides* in an effort to obtain a hardy aspen hybrid combining the wood characteristics required for match and veneer wood with resistance to heart rot.

Breeding of forest trees is also being stressed in Europe. Larsen, in Denmark, has been carrying on rather extensive breeding studies, especially from the standpoint of self-pollination, and has published his results in some detail. Von Wettstein, in Germany, has been interested in the hybridization of poplars, particularly for the production of trees especially suited to matchwood production. He has developed and described a method for the maturation of hybrid seed in artificial nutrient media. Liese, at Eberswalde, Germany, working with *Pinus montana* (Swiss mountain pine) and *P. sylvestris* (Scotch pine) failed to obtain hybrid seed between these species, which are considered to produce natural hybrids quite frequently. This failure, he concludes, may have been due to lack of "crossibility" between the particular strains used, and the use of other individuals might give positive results.

In addition to these strictly forest species, considerable breeding work has been done with various nut trees, such as the walnut, of which exceedingly vigorous hybrids are now in existence. This work is described in the article on nut-tree breeding elsewhere in this Yearbook.

The outstanding improvement apparent in natural and artificially produced hybrids between forest-tree species amply justifies particular effort in this direction.

VEGETATIVE PROPAGATION

Vegetative propagation will be of great value for the immediate utilization of exceptionally promising natural or artificially produced forest trees. The rapid improvement of horticultural trees has been possible because any new and improved type, hybrid or otherwise, could be immediately multiplied as a clone by grafting, budding, or other forms of vegetative propagation. With forest trees such as the poplars and willows, which can be propagated by cuttings, the tree breeder can utilize exceptional hybrids immediately with the assurance that the individual members of such a vegetative clone will exhibit the same inherent characteristics as the original tree, except for mutations in the body cells of various parts of the tree. These ordinarily occur so rarely that from a practical standpoint they are unimportant. By such methods it is possible to retain any excellent characteristic such as hybrid vigor—the exceptionally rapid growth often inherent in first-generation hybrids—or any new character that is due to an unfixed combination of complementary genes. Few forest trees, however, can be commercially propagated by cuttings, and although many species can be propagated vegetatively by grafting, budding, or layering, these methods are not feasible at present because of their comparatively high cost. It is essential to find cheaper

methods of vegetative propagation if select hybrids or strains are to be multiplied and utilized immediately for forestation planting.

A POSSIBLE APPROACH TO THE IMPROVEMENT PROBLEM

Seed Origin and Individual Seed-Tree Progeny Studies

A search of the literature may leave the impression that investigations in the past have too strongly stressed the subject of seed origin and seed-tree selection, and that the improvement of our forest trees along these lines will be exceedingly slow. But from the standpoint of immediate reforestation requirements, seed-origin and progeny studies are of the greatest importance if the errors responsible for the poor quality of many of the early European plantations are to be avoided. According to Baldwin, approximately 25 percent of the forest stands in Germany are inherently so poorly adapted to their environment that the Government has ordered clear cutting to prevent their regeneration.

A program for the improvement of our forest trees that is concerned with the immediate needs of general forestry may well contemplate studies on seed origin, delineation of races and strains of species and varieties, individual seed-tree progeny studies, and adaptability of exotics on a larger and more intensive scale than in the past. Although such studies are especially necessary to determine the best races or strains for forestation, the data derived from them will also be of great value for improving the inherent qualities of natural forest stands by silvicultural methods. Criteria for the selection of good breeding stock, that is, for differentiating environmental and hereditary characteristics, are essential to good silvicultural practice in our natural stands. Improvement cuttings, thinnings, and especially selective logging, are probably the forester's best approach to mass selection, which will improve the inherent quality of our wild forests in direct proportion to the ability of the silviculturist to identify the select stock and leave it for seed purposes.

There is evidence that in our forest trees many valuable inherent characteristics are still to be discovered and isolated. A list of characters in which differences between individual trees of the same species have been reported as apparently hereditary is included at this point, because it indicates the range of hereditary variation and the possibilities in selection from our present wild stocks.

Rapidity of growth.
Growth habit.
Crown and stem form.
Leaf size, form, and color.
Growth periods.
Nut qualities and length of catkin.
Yield and composition of resin.
Proportion of resin adhering to faces as "scrape."[5]
Color and correlated quality of wood.
Fiber length in wood.
Physical and chemical properties of wood.
Twisted grain in wood.
Resistance to frost, heat, light, and snow.
Resistance to disease and mistletoe.
Resistance to insects.

[5] This refers to the gum adhering to the wood exposed in turpentining, reducing the final yield appreciably.

These characters include not only those that are desirable from the standpoint of the forester (the producer), such as rapid growth and resistance to climatic conditions, disease, and insects, but also qualities important to the consumer, such as straightness of trunk and properties of the wood. Selection must be based on the requirements of the grower and the requirements of the user—so-called forest requirements and use requirements, respectively.

The silviculturist must look to the forest geneticist for possible correlations between readily recognized characteristics of the individual tree and its capacity for producing desirable progeny. Such correlations, even though they are only approximate, will be of great immediate value. This is especially true because the forester, managing a natural stand under a proper selection system, usually has an overabundance of seedlings, only a small percentage of which will be brought to maturity. If selection is for vigor of growth, the inherently vigorous individuals will normally take the lead and should make up a large proportion of the final crop. If other characteristics or qualities are desired, the forester using a selection system has opportunity to rogue his stand with each cutting or thinning, and undesirable individuals can be eliminated as their mature qualities become apparent.

Since the recognition of inherent quality is a key to the improvement of vast forest stands which for various reasons, such as inaccessibility or difficult environmental conditions, are not adapted to intensive forestry, well-planned investigations on this problem are justified. Much of the groundwork will not be strictly genetics. It will first be necessary to define clearly the desired characteristics or qualities. The relative desirability of particular qualities or characteristics will depend upon many things, including the species; the locality where it is to be grown; the purpose for which it is grown—watershed protection, soil-erosion control, tree crops or wood; and probable utilization—lumber, chemical wood, etc.

After the desired characteristics have been defined, methods for their accurate description or measurement must be devised. If measurement is not possible, then descriptions that will adequately bring out existing differences should be available. Rapidity of growth, usually a most important consideration in forestry, is easily measured. Measures for resistance to disease, insects, and climatic conditions will be fairly easy to develop. On the other hand, tree form or branching habit, very important from the standpoint of lumber quality, has been much debated but seldom adequately described or measured. Wood quality is even more elusive; "test-tube" methods for determining the physical and chemical qualities of wood are urgently needed. Tests that require cutting down the tree cannot be used to advantage by the forest geneticist, since a felled tree obviously cannot be used in breeding.

The progeny test is the generally accepted measure of inherent (breeding) quality. As applied to forest trees the method usually involves knowledge of the female parent only, since the seed is set by open pollination. Seed is collected from selected seed trees and the performance of the progenies of the individual seed trees is used as a criterion of breeding quality. This method eliminates the expense and

time involved in making controlled pollinations (fig. 9), but since the male parent is unknown the results must be interpreted with caution and can never provide exact genetical data on the mode of inheritance. This one-parent method may provide partially correct answers somewhat earlier than more exact methods, but a careful analysis of individual seed-tree progeny tests, which have been under way for a period of

Figure 9.—Controlled pollination technique developed for work with pines at the Institute of Forest Genetics. A finely woven canvas bag with transparent window is placed over the flowering branches before the female flowers come into bloom. The sulphurlike pollen of the desired species of pine is placed in the barrel of a hypodermic needle and injected into the bag containing the ovulate flowers. The transparent window in the bag enables the operator to determine when the flowers are in the receptive stage and ready to receive the pollen.

years, will be highly desirable before further extensive trials of this kind are started.

Progeny tests involving full control of parentage are required to provide accurate data on heritability and mode of inheritance of particular characteristics. With this method both the male and the female parents are known. Self-fertilization, where possible, will be the quickest method of evaluation, but it is to be recognized that selfing in plants that naturally cross-breed often leads to degenerate lines, with loss of vigor. This must be considered in pure line breeding with forest trees which are apparently continually cross-pollinated.

Selective Breeding and Hybridization

Improvement by selection of the best individuals or strains from the wild stock is limited in scope. This procedure can hardly result in improvement of our best forest trees in the strict sense of the word, since the essence of the selection process is a sifting out of undesirable types and a segregation of the best strains already in existence.

Hybridization and selective breeding aim beyond this point and attempt to develop new types, which combine the desirable characteristics present in two or more individuals often widely separated geographically and sometimes racially. This possibility can be demonstrated in the hybrid progeny of a controlled cross-pollination, carried out at the Institute of Forest Genetics, between *Pinus atten-*

Figure 10. Hybrids of knobcone and Monterey pines combine the frost resistance of one species and the vigor of the other. The short tree on the right represents the hardy but slow-growing knobcone pine. Beyond it are two trees of the badly frosted but rapid-growing Monterey pine. On the left are three hybrids of these two species. They have about the same vigor as their pollen parents, the Monterey pine, and are practically as hardy as their seed parent, the knobcone pine. All trees are 4 years old from seed.

uata (knobcone pine) and *P. radiata* (Monterey pine), which combine the rapid growth of the pollen parent with the frost resistance of the seed parent (fig. 10); or in the Dunkeld larch, which is said to combine the excellent growth qualities of the European larch with the resistance to larch canker inherent in its Japanese parent. Cross-breeding may also result in the creation of entirely new characteristics, the expression of combinations of genes that would never occur under natural conditions. As has already been said, hybridization and breeding have infinite possibilities, but they are only at their beginning in forestry.

A proper appreciation of breeding methods must be based upon the realization that the plant breeder is concerned with individual plants; that particular characteristics or qualities of the individual are of primary importance; and that the factors or combinations of factors in the germ plasm, which are responsible for the particular characteristics, are the raw materials that the breeder must shape into his ideal plant. With this in mind it is obvious that the most rapid progress in forest-tree improvement necessitates accurate information on the expression and behavior of the hereditary units in our various forest-tree species.

Mass Selection

In mass selection, groups of plants with more or less uniform characteristics are permitted to intercross. Close control of parentage is impossible, and gradual improvement results from continued selection of breeding stock on the basis of apparent quality. Improvement is

usually rather slow and the method does not provide accurate data that can be utilized for further breeding. The results attained depend to a considerable extent on the judgment of the breeder in selecting seed plants, and especially on his ability to distinguish between the effects of heredity and of environment. As noted previously, for the present this method seems best adapted to the improvement of natural stands that are to be handled under a selection system.

One-Parent Progeny Tests

The evaluation of the inherent quality of an individual tree on the basis of the progeny derived from uncontrolled pollination has already been discussed. The fact that only the female parent is known and that the unknown male parent has contributed half the germ plasm of the progeny considerably restricts any interpretation of the results. The method can probably be recommended only for preliminary survey purposes or where personnel is inadequate for the application of a more accurate procedure.

Pedigree Breeding Within and Between Varieties, Species, and Genera

Pedigree breeding with full control of parentage has been described in many of the articles in this and the 1936 Yearbook of Agriculture. Here both parents are known, and the progeny derived from selfing and from well-planned crosses provide an accurate measure of the respective parental germ plasm. Investigation by this method will not only determine which characteristics are inherent, but will also indicate the mode of inheritance—information that is indispensable for far-reaching improvement by intensive breeding and hybridization. The following discussion indicates pedigree methods applicable to forest trees.

Pure-line breeding, by selfing, is usually the most rapid method for the evaluation of hereditary characteristics. This will be possible only with trees that are hermaphrodite and self-fertile. In breeding trees that produce male and female flowers on separate individuals, or hermaphrodite trees that are self-sterile, crossing between selected individuals is necessary. With trees of this nature the nearest approach to pure-line breeding is to cross parents possessing the same characters, that is, breeding within a strain, variety, or species. Pure-line breeding and cross-breeding within a variety or strain will provide fundamental genetical data for the evaluation of inherent quality and the mode of inheritance, and may also provide superior races and strains for forestation. These superior types will be a source of superior germ plasm of known breeding value for further hybridization and breeding.

Combinations of desirable characteristics and modifications or new expressions of characters, due to new combinations or rearrangements of the determiners of heredity, are possible by cross-breeding between pure lines or varieties (intervarietal or intraspecific hybridization). Intervarietal crosses ordinarily represent the least difficult kind of hybridization. Varieties usually cross quite readily and produce fertile offspring. Valuable results may be apparent in the F_1 or first hybrid generation, and segregation in the F_2 or second generation (F_1 plants selfed or crossed) will produce new combinations from which the best individuals can be chosen for further selective breeding.

Crosses between different species of forest trees—a more remote relationship than between varieties—offer interesting possibilities. Such interspecific hybridization is often complicated by the fact that two species are difficult to cross, or by the partial or complete sterility of the resulting hybrids. If two species cannot be crossed directly it is at times possible to include them in the parentage of the final hybrid by breeding through a third species. In fact the utilization of three or more species in the breeding of daylilies has produced particularly valuable hybrids.

The first-generation hybrids of two forest-tree species are often quite uniform and more or less intermediate between the parent species. Segregation and recombination of characteristics occur in the second generation, and it is this generation that provides a very wide diversity of material for selective breeding. The procedure indicated is, therefore, (1) a small first-generation population, but (2) a large second-generation population, with (3) selective breeding continued with the most promising individuals of the second generation.

Interspecific hybridization of our forest trees is entirely justified, because it offers immediate improvement by combinations of desirable characters and the possibility of entirely new characteristics or qualities resulting from combinations of determiners that have never before been combined in any germ plasm. Many first-generation hybrids are more vigorous than either of their parents. This so-called hybrid vigor and any other valuable character can be maintained and utilized immediately if vegetative propagation is possible. Hybridization followed by polyploidy has also created individuals with unusual chromosome numbers that are superior to their parents and have their characteristics "fixed" so that they come true from seed.

Genera are, of course, even more distantly related than species. The comparatively few intergeneric plant hybrids that have been produced up to the present time have not been of practical value. Intergeneric hybridization is very greatly limited by specific differences in the requirements for fertilization inherent in distantly related plants. Furthermore, the progeny are seldom fertile. In spite of the difficulties involved, crosses between different genera may lead to valuable results, and excursions in this direction are warranted.

The Time Element in Tree Breeding

The improvement of forest trees by breeding and selection might appear, at first sight, to require centuries for completion. But although the work often requires a considerably longer time for the successful production of improved stocks than similar work with annual plants, various short cuts are possible.

The time element in breeding is dependent among other things on the relative age at which the individuals begin to bloom. Many trees produce flowers early in life —7-month-old chestnut seedlings occasionally bloom in nursery beds; fruit is often produced on chestnut trees before they are 5 years old; 4-year-old pines have been observed to mature cones; first-generation poplar hybrids 7 years old from seed have produced flowers and fruit. The blooming of more slowly maturing trees can usually be hastened by top-working or grafting on closely related mature individuals, and possibly in some species by

ringing, a light girdling of the trunk. Further work to determine the possibility of lowering the blooming age would be well worth while, since early blooming permits further cross-breeding or inbreeding and eventually speeds up the entire improvement program.

In order to take advantage of early blooming, correlations between juvenile and mature characteristics must be discovered. The fact that a tree blooms at an early age is of no value unless its characteristics at maturity can be predicted with fair accuracy. Such qualities as resistance to disease and winter hardiness can usually be determined with young trees, but in breeding for good forest form (habit of growth) it will be necessary to recognize and select for further breeding the young individuals that will develop good form at maturity.

The possibility for early results is indicated by the fact that selective breeding with daylilies, based on a knowledge of the mode of inheritance within the group, has fixed new combinations of germ plasm, derived from as many as four distinct species, into new types in five generations (Stout, 1936).[6]

Increased Chromosome Numbers, Polyploidy, Aneuploidy, and Mutations

Many valuable types of cultivated plants have arisen through an increase of chromosomes, originating in the somatic (body) cells, in the germ cells, or in the earliest divisions of the fertilized egg. The increase may consist in the duplication of a single chromosome, an unbalanced condition referred to as aneuploidy; or the chromosomes may be duplicated in multiples of the basic number (polyploidy). There may be multiplication of the chromosomes of a single individual (autopolyploidy), or a multiplication of both of the parental chromosome complements of a hybrid (allopolyploidy). Individuals with unbalanced chromosome complements may be maintained and multiplied as clones if vegetative propagation methods can be used.

There is evidence that merely a quantitative increase in chromatin material may be responsible for wide differences in characters that are of great practical value, and that polyploidy in hybrids, involving a quantitative increase in the chromatin material received from both parents, can produce new types as distinct as many of our present species. Polyploidy may result advantageously in (1) increased vigor; (2) increased variation; certain types of polyploidy may also give (3) increased fertility; (4) stability—that is, new types may breed true. On the other hand, polyploidy is sometimes directly responsible for increase in cell size, a contingency that is of particular significance since the chief product of forest trees is wood. An increase in the size of the wood fibers would be detrimental to the physical properties of some woods and would limit the use of others now used in the manufacture of particular grades of paper.

Of especial interest to forest-tree breeders are the facts that polyploidy has been induced by physical treatment of both somatic (body) and germinal tissue and by hybridization, and that balanced polyploids may breed true. If a superior self-fertile individual of this nature can be developed by physiological methods or by hybridization, it can immediately be propagated by seed. Such a strain

[6] See Bibliography, published in the Yearbook separate of this article.

would probably not cross readily with the native species and might thus maintain itself unmixed (homozygous) under natural conditions. The possibilities justify intensive effort directed toward the creation of polyploid strains.

New variations of the nature of mutations and bud sports, involving basic changes in the chromosome complement other than those due to duplication, occur occasionally in forest trees. The Lombardy poplar is said to be a mutant form of the European black poplar (*Populus nigra*) and the weeping beeches and birches are probably of similar origin. Although such variations have been primarily of value as ornamentals, it is possible that individuals of particular value for forestation purposes may be discovered.

Advantages in the Use of Vegetative Propagation

If vegetative propagation is feasible, any superior individual can be multiplied immediately and its characteristics perpetuated by the establishment of a clone By vegetative propagation the breeder can

Figure 11.—One season's growth from roots of poplar hybrids cut back annually for the production of cuttings. The measuring rod is 9 feet high.

take advantage of the excellent individuals that may be produced at any stage of the breeding work, and since the components of the germ plasm are maintained in the somatic condition, the difficulties due to segregation of superior chromosome combinations are eliminated. Many so-called species are actually clones, and the uniformity among the individuals is due to the fact that the genetical complex is always passed on exactly as it was in the original plant.

Vegetative propagation does not lead to degeneration in clones. Investigations on cases of supposed senescence in clones have proved

that outside agencies such as environment or disease-producing organisms have been responsible.

The most promising hybrids produced in connection with the breeding project of the Oxford Paper Co. have been rapidly multiplied from cuttings at a unit cost lower than that of northern-grown nursery stock. Some idea of the rapidity of propagation by means of dormant cuttings may be gained from the fact that in Maine, with a comparatively short growing season, a 1-year-old poplar hybrid will produce 10 to 20 cuttings, at 2 years, 40 to 60 cuttings, and that after 3 years it will continue to produce 100 to 200 cuttings annually (fig. 11). If necessary, the rate of multiplication can be further increased by propagation from softwood cuttings. By this method small twigs 4 to 6 inches in length, cut from the mother plant throughout the growing season, are rooted in shaded, moist sand beds.

Figure 12.—Controlled hybridization in pines involves physical difficulties. This 77-foot ponderosa pine has 100 bags protecting the ovulate flowers from wind pollination.

Intensive investigation to develop a cheap method for the vegetative propagation of forest species that cannot now be economically reproduced in this way is fully justified; the best of our present wildlings and the elite individuals produced through breeding can then be utilized without further delay.

Need of Developing Technique

As in every new line of research, technical difficulties must be overcome before extensive breeding work can be undertaken. The breeder of forest trees is not only faced with the physical difficulties incident to the necessity of working with flowers at the tops of large trees (fig. 12), and often on the outside branches, but he is also handicapped at the present time by lack of accurate information essential to his work. Practically nothing is known of flower behavior, pollen-storage possibilities, artificial pollen-germination methods, sterilities, and incompatibilities in forest trees, and the affinities between species.

Accurate and detailed data on the flowering period of parent trees are essential for the successful planning of a breeding project. Information on blooming dates is not always sufficient; the receptive period of the female flowers is of vital importance in breeding. Where dichogamy, or the ripening of male and female organs at different times, occurs, it often necessitates storing pollen until it can be used, and since pollen viability in different species is known to vary from a few days to over a year, data on this point should be available. Assuming that the pollination has been made with viable pollen at the proper time and under favorable climatic conditions, incompatibilities or sterilities may still cause failure, and success can be attained only through a thorough understanding of such conditions.

The breeder of agricultural plants usually has more or less proven varieties and strains available that can be grown in adjacent plots in his experimental grounds. The breeder of forest trees must work with a wide diversity of species and varieties and often with widely scattered parent stocks—desirable parent types may be located hundreds of miles apart, and at best they are seldom within walking distance. Crossing such trees often requires the development of a new technique.

FUNDAMENTAL INVESTIGATIONS[7]

FUNDAMENTAL genetical studies should certainly be started with forest trees. Chromosome studies and other cytological work necessary to a thorough understanding of the particular physical process involved in the transmission of hereditary characteristics in trees will be indispensable to the tree breeder. Cytological data will be an immediate necessity for effective work directed toward the compounding of polyploids. The solution of many problems will require the combined efforts of the geneticist, the cytologist, and the physiologist.

The forest geneticist should lay a broad foundation for such fundamental studies, but in doing so he should not overlook the fact that much of his early work must of necessity be more or less empirical in nature. It is generally recognized that the mode of inheritance of any particular character can seldom be predicted from a cytological study of the parents used; only actual crossing can supply the answer. It will be largely on the breeding work of the forest geneticist of today that the forest geneticist of tomorrow can safely continue his fundamental research, with the assurance that his line of attack is in the right direction.

A questionnaire on the subject of improvement in forest trees, which was submitted in connection with this Yearbook to various individuals and organizations both in the United States and abroad, asked for an opinion on the outstanding technical and practical problems that remain to be solved. In order to present the views of individual workers in various parts of the country with respect to their particular problems, it seems advisable to include their recommendations on genetical problems verbatim.

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[7] The following section is intended primarily for students and others professionally interested in breeding or genetics.

Lloyd Austin. California Forest and Range Experiment Station, Institute of Forest Genetics, Placerville, Calif.

Adaptability of selected strains and progenies.—While quite a little preliminary work has been done by the institute and other organizations in testing in a general way the adaptability of various forest species, only a bare beginning has been made in the formidable task of adequately testing and retesting the various selected strains and progenies of these species that are gradually being discovered. There can be no one best strain for all localities, and, as superior types are isolated by progeny tests and other methods, it will become imperative to try these out in a comprehensive way and under various climatic and soil conditions, so that eventually the best forms for each locality will be definitely known.

Hybridizing within species to combine vigor and cold-hardiness.—The institute's results seem to indicate that, at least in the case of *Pinus ponderosa,* most of the seed trees having the greatest inherent vigor will probably be found at relatively low elevations. Although proof is not yet available, it seems highly probable that these low-altitude forms will lack the degree of inherent cold-hardiness possessed by the forms from the higher elevations where much lower temperatures are encountered. This opens up a most promising line of genetical research in which artificial crosses would be made between low- and high-altitude strains, utilizing as parents in both cases the individual seed trees that the progeny tests show to be hereditarily superior. In this way it should prove possible to combine the rapid growth rate of one form with the desired cold-hardiness of the other, and thus greatly increase the adaptability and usefulness of the vigorous types. The institute has already accomplished practically this same combination of characters in the case of its cross of *P. attenuata* and *P. radiata,* and it should prove much easier to cross different altitudinal forms of *P. ponderosa* than to cross distinct species, which is nearly always difficult of accomplishment.

Improving the quality of seed from selected native seed trees.—Another promising line of genetical inquiry well worthy of investigation would consist in making tests in relatively isolated field plots to determine the practicability of using a carefully regulated thinning to improve the quality of the seed from the germinally superior individuals. The plan would be to cut out all those seed trees that the progeny tests show to be inferior. In this way subsequent natural cross-pollination would take place largely between the better types and seed with improved heredity should result. Such seed would be highly valuable for actual work in reforestation.

Roy L. Donahue. Mississippi State College, State College, Miss.

I would say that the needs for this region in particular with reference to forest genetics should include a testing of the various strains of black locust, especially different strains varying as to seed source.

Another type of research needed in Mississippi as well as throughout the entire South is in relation to the selection and breeding of a first-class Christmas tree. At the present time Christmas trees of excellent quality are imported from as far away as the West coast.

Duncan Dunning. California Forest and Range Experiment Station, Berkeley, Calif.

Studies should be made of the heritability of crookedness, excessive branching, spiral grain, and susceptibility to diseases.

Arthur H. Graves. Brooklyn Botanic Garden, Brooklyn, N. Y.

The most important of these requirements for rapid progress in forest tree improvement is reproduction by asexual methods cutting, layering, budding, and grafting.

C. Heimburger. Petawawa Forest Experiment Station, Chalk River, Ontario, Canada. Urgent research problems:

The finding of a suitable strain of Norway spruce for pulpwood production, especially for the spruce regions in eastern Canada.

The finding of suitable strains of Scotch pine to replace jack pine, on sites not suitable for other more valuable native pines.

The production of a fully hardy rapidly growing aspen hybrid, combining the useful characters of the native aspens with added resistance to heart rot and better wood quality for the production of match stock and veneer.

A suitable propagation method for aspen poplars and their hybrids, better than the usual root-cutting methods.

Richard E. McArdle. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Other practical problems which demand solution involve the development or isolation of drought-resistant strains of native species (particularly ponderosa pine) for planting in the sand hills of the Plains States and in the high plains dry-land country immediately east of the mountains; determination of the best strains of Engelmann spruce and possibly other species for planting on denuded subalpine sites in the spruce type in Colorado, also in the bristlecone pine and limber pine types where administrative restrictions have been imposed upon the planting of native soft pines because of the blister-rust menace; improving lodgepole pine from a pathological standpoint to cut down losses in merchantable stands. While these problems are practical in their scope, their solution can follow only along highly technical lines of approach. This will require, therefore, the solution of technical problems either directly or under the supervision of qualified geneticists.

T. E. Maki. Intermountain Forest and Range Experiment Station, Ogden, Utah. Urgent research problems:

Determination of the inherentness of heavy or light seed producers.

Determination of vigor, natural pruning habit, etc., of progeny from different tree and age classes.

F. I. Righter. California Forest and Range Experiment Station, Institute of Forest Genetics, Placerville, Calif.

Breeding with polyploids.—In pine breeding projects the problem of inducing tetraploidy in hybrids may well be regarded as second to none in importance. The production of such forms, which, having their origin in hybridization, are yet something more than hybrids—namely, amphidiploid hybrids—will yield the following advantages: (1) Prolonged and costly selection tests of the F_2 and succeeding generations would be avoided; (2) such forms often are more vigorous than the parental species; (3) they are endowed with higher degree of fertility; (4) insofar as practical purposes are concerned, they breed true; and (5) when they, in turn, are hybridized the F_2 generation will consist of greater varieties of new forms for investigation than does the F_2 of the ordinary species or varietal cross.

Polyploidy has not been reported for the pines, and it probably will be necessary to induce tetraploidy before any further breeding with polyploids will be possible; however, the tetraploids should constitute sufficient justification in themselves for work in this field. The possibility of realizing the benefits which may be expected from the production of amphidiploid hybrids is not more remote than is that of achieving comparable results through selection tests subsequent to hybridization. In fact, the latter method of proceeding may well be regarded as the last desperate resource in the field of hybridization with pines, whereas the former offers such valuable results that its immediate adoption is fully justified.

Tetraploidy has developed in sterile species hybrids spontaneously but such appearances have been so rare that it will not be practicable for the pine breeder to rely on the production of such forms through the operation of Nature alone. Artificial means are practically a requisite for such work. Fortunately, means of inducing tetraploids have been developed. The chief method developed thus far consists of subjecting the zygote to heat treatments during the first few cell divisions following fertilization. Under the influence of such treatments a newly formed embryo may undergo nuclear division without the laying down of a dividing wall. This process results in the formation of a cell having the double number of chromosomes. The further growth of the embryo results in an individual that is entirely tetraploid. Attempts to induce tetraploids in hybrids may prove difficult at first, because of the difficulty of ascertaining when fertilization occurs,

for in most of the pines fertilization occurs about a year after pollination; however, the problem should yield to the combined attacks of the geneticists, the cytologist, and the physiologist.

Cytological, taxonomical, and physiological studies.—Cytological, taxonomical, and physiological studies of the genus *Pinus* will contribute immeasurably to the progress of the work of breeding superior timber trees, because they ramify into all phases of the work. Such studies will be started in the near future.

Paul O. Rudolf. Lake States Forest Experiment Station, St. Paul, Minn.

As far as forest genetics goes, the field has barely been scratched. So many problems remain to be solved that it is difficult to know where to begin in listing what remains to be done.

From the practical standpoint it seems desirable to extend source-of-seed tests to include all species used in forestation work to indicate within what limits seed can safely be used in other than native localities for various species. The selection of individual trees and stands of particularly desirable characteristics, followed by the determination of the extent to which these characteristics are heritable by their progeny, is another useful field of investigation. Cross-breeding and hybridizations which have been begun with certain early-maturing species of *Populus*, *Salix*, and *Larix* here and abroad might well be extended to other species in general although the immediate practical value may not be as great as for other studies.

In the field of pure genetics much of value might be accomplished by a study of the mechanics of inheritance for important tree species particularly with a view to determining how certain desired characteristics are transmitted and to what extent such functions may be modified or controlled.

Philip C. Wakeley. Southern Forest Experiment Station, New Orleans, La.

Further work upon the pines (to say nothing of the hardwoods) is urgently needed in:

a. Effect of climatic-zone source of seed.
b. Effect of major soil type source; e. g., deep sands.
c. Effect of female parent source alone on progeny (of direct application in seed collection).
d. Effect of both parents upon progeny (of direct application in marking for natural reproduction cuttings).
e. Development of very tall strains for high yields, structural timber, and piling.
f. Development of strains high in naval stores yield.
g. Development of brown spot-resistant *P. palustris*, windfirm *P. caribaea*, and tip moth-resistant *P. taeda* and *P. echinata*, for artificial reforestation.

APPENDIX

As a part of the cooperative survey of plant and animal improvement, a comprehensive questionnaire requesting information on investigations pertaining to improvement in forest trees was sent to approximately 150 institutions and private agencies in various parts of the world. Summaries of the reports received from those organizations or individuals engaged in work of this nature are included here. The replies received present a rather complete account of forest-tree improvement work in progress throughout the United States, but the replies from foreign sources are rather limited.

United States—Federal Agencies

Bureau of Plant Industry, Division of Forest Pathology

3. Hybridization

Progeny of the following crosses, being grown for forest-tree improvement, are under observation:

Castanea mollissima × *C. dentata*, 272 seedlings 1 to 8 years old.

C. crenata (forest types) × *C. dentata*, 33 seedlings 1 to 4 years old.

C. crenata (forest types) × *C. mollissima*, 44 seedlings 1 to 5 years old.
C. mollissima × *C. henryi*, 16 seedlings 1 to 9 years old.
C. crenata (forest types) × *C. henryi*, 3 seedlings 1 to 2 years old.

In general, hybrid vigor is present in these first-generation trees in the order as listed.

Progeny of the following crosses apparently should be valuable in the production of mast crops and for soil conservation planting:

C. pumila × *C. seguinii*, 21 seedlings 1 to 5 years old.
C. mollissima × *C. seguinii*, 19 seedlings 3 to 6 years old.
C. crenata × *seguinii*, 24 seedlings 1 to 6 years old.

Reciprocal crosses are usually made as a matter of routine. From the genetic viewpoint no significant differences have been found in their progeny. Seedlings of crosses with a dwarf Chinese chestnut, *C. seguinii*, tend to be everblooming in habit, a dominant character inherited from that species. Additional crosses are being made between the several American chinquapins and the various true chestnuts from Asia. Here again selections will be made of individuals suitable for mast-crop production and soil-conservation planting, but such selections are not expected to carry the everblooming habit.

Present work is now largely confined to the production of second-generation stock and incidentally to the study of genetic phases of the problem with special regard to the inheritance of resistance to the chestnut blight.

Forest Service, Appalachian Forest Experiment Station [8]

1. Seed Origin

Robinia pseudoacacia (black locust)

One-year-old seedlings from seed collected from seven Appalachian sources (West Virginia, Virginia, North Carolina, 1,800 to 3,000 feet elevation) were set out in test plantations at Bent Creek in 1935. Seed from an additional five sources (three foreign, two American) was used to establish test plots in South Carolina, West Virginia, North Carolina, and north Georgia in 1936. In both experiments significant differences between the average height of seedlings from different sources were observed at the end of the first season's growth. Some difference was also indicated in form of bole.

In the fall of 1935, 20 superior and 20 average seedlings were selected in each of 10 nurseries (in North Carolina, South Carolina, Tennessee, Mississippi, Virginia, and West Virginia). These were planted in test plots in the Bent Creek Experimental Forest in 1936 to determine the possibility of selecting superior strains from 1-year-old seedlings.

2. Individual Seed-Tree Progeny Tests

Pinus taeda (Loblolly Pine)

Seedlings from 122 individual seed trees were out-planted in 1936 for progeny study. The purpose of this experiment is to determine the effect of the female parent on the germination and growth of seedlings, with the ultimate aim of determining the desirable characteristics of loblolly pine seed trees.

California Forest and Range Experiment Station, Institute of Forest Genetics

1. Seed Origin

Extensive tests of species and geographical races are well under way. The arboretum contains approximately 100 species and named varieties of the genus *Pinus* and innumerable climatic forms of many of these species; seed has been obtained from 40 countries. Growth records, taxonomic records, phenological records, injury records, and seed, sowing, and germination records are taken on all of these test trees, which range in age from 4 to 15 years. Among the fastest growing species so far tested are *P. radiata* (Monterey pine), *P. pinaster* (cluster pine), *P. taeda* (loblolly pine), *P. coulteri* (Coulter pine), *P. patula* (Toluca pine). In most tests *P. radiata* has surpassed all other species in rate of growth, particularly in height growth.

The great majority of all the pine species tested have possessed sufficient cold-hardiness to enable them to survive at the institute at Placerville, Calif., where

[8] At Asheville, N. C.

the lowest temperature on record is 16° F. Exceptions have occurred in the case of certain tropical species, such as *Pinus tropicalis*, *P. insularis*, *P. canariensis*, and *P. merkusii*. These species do not seem to possess enough inherent resistance to cold to be of practical value in any of the important forest regions of the United States, but they are of interest to tree breeders who may wish to hybridize them with hardier species.

Tests with approximately 30 species of pine are under way in cooperation with numerous organizations (31 in the United States and 1 each in England, Scotland, and Denmark) to determine the adaptability of the various native and foreign species.

In addition to the work with pines, 35 species of conifers, representing 17 genera, and 20 species of hardwood trees, 13 genera, are included in the arboretum.

These investigations will eventually indicate the value and adaptability of geographic races and strains of many important timber trees, and the arboretum will be a source of superior germ plasm for future selection and breeding work.

2. Individual Seed-Tree Progeny Tests

Progeny tests have been undertaken with 10 species and varieties of pines. All seed is collected from tagged seed trees, which are fully described and have their location recorded in map form. Seed has been gathered from a total of 2,609 separate trees located in 289 field plots. Many thousands of seedlings have been grown in the nursery and of these 1,843 progeny trees have appeared worthy of further trial in forest plantations to test the permanence of the early differences apparent in the nursery.

As rapidly as the desirable seed trees are discovered, they become for many years potential sources of relatively large quantities of superior seed for practical reforestation. Trees selected in this way are also valuable for use in breeding experiments designed to develop still better types.

P. ponderosa (ponderosa pine)

The largest single progeny test was started in 1929 with seed from 742 individual trees of this species and its varieties *scopulorum* and *jeffreyi*. (*Pinus jeffreyi* is considered a separate species by Sudworth in his Check List of the Forest Trees of the United States.) The seed trees represented in this test are scattered over 60 counties in 12 Western States and British Columbia.

Results already indicate that within this species and its varieties there are innumerable local strains, each with distinct morphological and physiological characteristics. Even within a local geographical strain, individual seed trees vary strikingly in their ability to produce seedlings that are superior in vigor and in habit of growth.

Although the hereditary vigor of ponderosa pine in the central Sierras of California tends to decrease markedly with an increase in the elevation of the seed source, certain individual seed trees have been found at relatively high elevations which, contrary to the general tendency, have high inherent vigor. These are of outstanding value since they probably have the ability to produce offspring that will be both fast-growing and cold-hardy.

Eldorado County, Calif., seems to be about the center of the optimum belt for ponderosa pine, and an intensive progeny test is to be started in the spring of 1937 using seed already collected from about 1,000 trees growing in this county and closely adjoining areas. Seed-collection activities have been so directed that there has resulted a relatively complete sampling of the local strains within this limited area. The field plots are distributed over an altitudinal range of more than 8,000 feet, extending from an elevation of 150 feet up to 8,400 feet.

It is hoped from these various progeny tests to determine whether or not there are any correlations between the visible characters of the seed trees and the nature of their progenies, and to ascertain any relationships that may exist between the environment of a seed tree and the growth, hardiness, etc., of its progeny.

Juglans (walnuts)

Walnuts are being studied primarily from the point of view of developing superior timber trees, and their nut-producing characteristics are a secondary consideration in these experiments. Tests have been undertaken with the progenies of 272 individual trees of 16 species and hybrids of walnuts. After growing the progenies for 2 years in the nursery, 421 seedlings were selected and

set out in permanent plantations. There have been marked differences in the growth of the different progenies.

In some cases natural cross-pollination between species apparently took place during the spring prior to the collection of the nuts, for certain nonhybrid seed trees yielded progenies that were partly hybrid in nature. The nuts were graded into three sizes before sowing, and it was later discovered that most of the hybrids, some of which were very vigorous, came from the large nuts. Hybridization apparently stimulated the development of the nuts, and this may provide a simple method for selecting a high proportion of naturally hybridized nuts from walnut trees exposed to pollen of other walnut species.

3. Hybridization

Controlled hybridization has been a very important part of the work carried on at this station.

Progeny of the following artificial crosses (made at the institute) are under observation:

P. attenuata (knobcone pine) × *P. radiata* (Monterey pine). Hybridity certain. Progeny, 8 years old, shows rapid growth of pollen parent combined with frost resistance of seed parent. Appears to be weakly fertile. Twenty-eight trees.

(*P. attenuata* × *P. radiata*) × self. (F_2) hybridity certain. Progeny 3 years old. Five trees.

P. caribaea (slash pine × *P. taeda* (loblolly pine). Hybridity probable. Progeny 3 years old. Ten trees.

P. echinata (shortleaf pine) × *P. taeda*. Hybridity probable. Vigor of 2-year-old progeny exceeds that of seed parent. Fourteen trees. Seedlings now 3 years old.

P. ponderosa var. *jeffreyi* × *P. ponderosa*. Hybridity certain. Vigor of 3-year-old progeny greatly exceeds that of seed parent. A potentially valuable cross.

P. rigida (pitch pine) × *P. taeda*. Hybridity probable. Four trees. Age 3 years.

The following artificial crosses were made with various species and varieties of *Juglans* in 1927:

J. hindsii × Royal hybrid; 12 hybrid seedlings obtained.
Royal hybrid × Royal hybrid; 7 hybrid seedlings obtained.
Royal hybrid × *J. mandshurica:* 1 hybrid seedling obtained.
Royal hybrid × *J. regia;* 3 hybrid seedlings obtained.
J. hindsii × *J. hindsii;* 3 seedlings obtained.
Royal hybrid × *J. hindsii;* 1 hybrid seedling obtained.

Central States Forest Experiment Station[9]

1. Seed Origin

Robinia pseudoacacia (black locust)

Experimental work was started in 1935 with approximately 22 strains of black locust, including the shipmast locust (var. *rectissima*), in a search for strains resistant to locust borer.

Yellow pines

Work of a minor nature is in progress with local strains of shortleaf, pitch, and Virginia pines.

Intermountain Forest and Range Experiment Station[10]

1. Seed Origin

Pinus ponderosa (ponderosa pine)

Some experimental work on importance of seed origin is being carried on but work is too recent for definite observations.

Future plans call for investigations on regional and altitudinal strains of this species.

[9] At Columbus, Ohio.
[10] At Ogden, Utah.

Lake States Forest Experiment Station [11]

1. SEED ORIGIN

Pinus resinosa (Norway pine)

Three plantations each containing progeny from 154 seed sources (Lake States, Pennsylvania, New York, New England, Quebec, Ontario) were established in 1931 and 1933. Seed collection was mostly from "individual tree" or "small group" but some "limited locality" and general collections are also represented. Differences are already apparent in vigor, winter hardiness, and drought resistance.

Pinus sylvestris (Scotch pine)

Progeny from 27 seed sources (United States and foreign) were included in the plantations of Norway pine (1931 and 1933). Differences have been observed in the nursery and in the field between northern and southern stocks in size of seedlings and color of foliage—stock from southern sources is larger and tends to have darker green foliage Northern stocks showed markedly superior winter resistance, 1935–36.

Picea (spruce)

In a search for fast-growing spruce for pulpwood, plantations of nine different spruces were established in 1936. The following species were used: *P. glauca* (white spruce) six seed sources; *P. excelsa* (Norway spruce) six sources, mostly from the Union of Soviet Socialist Republics; *P. rubra* (red spruce) two sources; *P. glauca albertiana* (Alberta spruce); *P. mariana* (black spruce); *P. glehnii* (Sakhalin spruce); *P. orientalis* (Oriental spruce); and *P. omorika* (Serbian spruce) Seed of the last five each from one source.

2. INDIVIDUAL SEED-TREE PROGENY TESTS

Fraxinus pennsylvanica lanceolata (green ash)

Progenies of 83 individual trees (from North Dakota, South Dakota, Iowa, Nebraska, Kansas, and Oklahoma) were grown in two nurseries (York, Nebr., and Denbigh, N. Dak.). Variations between individual progenies were apparent in the nursery; seed from the northern area exhibited slow germination and growth. Seedlings from northern stock were much smaller, with smaller, darker green leaves, and shorter growing periods than southern stock. Transplants of the York stock were field-planted in Nebraska in the fall of 1936, but are insufficient in number to give conclusive results.

Artificial drought tests indicated a definite decrease in drought resistance from north to south and from west to east (definitely correlated with climate). The greatest difference was observed between plants from the northwest portion of North Dakota and the eastern portion of Nebraska, Kansas, and Oklahoma. The evidence indicates that there are inherently different climatic races. Local variations within a single subdivision of the plains region were also observed.

Pinus resinosa (Norway pine)

Approximately 100 of the 150 seed lots mentioned under Seed origin were from individual seed trees. A few of the individual progenies are sufficiently outstanding to indicate that selection and breeding might produce a superrace of Norway pine.

Pinus sylvestris (Scotch pine)

Some 20 of the 27 seed lots obtained for provenience study were from individual seed trees growing in the Lake States. No significant differences have been observed to date.

Northeastern Forest Experiment Station [12]

1. SEED ORIGIN

Pinus sylvestris (Scotch pine)

Two-year-old seedlings of two strains of Scotch pine, Riga and Austrian, were outplanted in 1925 on the Mount Toby Demonstration Forest in Massachusetts After 11 years the Austrian Scotch pine has made 2 to 3 feet better height growth

[11] At St Paul, Minn.
[12] At New Haven, Conn.

and greater diameter growth than the Riga strain, and it appears to have a superior stem form.

Studies are under way to determine whether a single vigorous stock of Scotch pine is suitable for planting in all parts of the Northeastern region. In 1932, 2–2 planting stock from a single seed source (Booneville, N. Y.) was planted in 10 test plots of 1,200 trees each throughout the Northeastern States. Additional plantings were made in 1934 using 1–2 and 2–0 stock from the same source. No significant results have been noted up to the present time.

A rather comprehensive forest-genetics project is now being started. It is anticipated that this project will include practical and fundamental research on seed origin, adequate progeny tests, selective breeding and hybridization. Although the primary emphasis will probably be placed on deciduous forest trees, some work with conifers, particularly with reference to disease and insect resistance of native species, will undoubtedly be advisable. The station also expects to cooperate with the Oxford Paper Co. in continuing the valuable hybridization work with poplars started by that organization in 1924.

Northern Rocky Mountain Forest and Range Experiment Station [13]

1. Seed Origin

Pinus ponderosa (ponderosa pine)

Twenty-two experimental plots in northern Idaho contain progenies from seed collected in 22 geographic localities in Oregon, California, Idaho, Washington, Montana, South Dakota, Colorado, Arizona, New Mexico, and Utah. The trees are now 23 to 27 years old from seed

Figure 13 —Racial differences in ponderosa pine: *A*, The open, plumelike arrangement of long, slender needles of the North Pacific and Northern Rocky Mountain races is easily distinguished from *B*, the compact and bushlike growth of short, stout needles of races from the east slope of the Rocky Mountains.

[13] At Missoula, Mont.

A number of distinct races have developed under natural conditions in ponderosa pine, which is widely distributed throughout the Western States and is subject to a great diversity of environmental conditions (fig. 13). Progenies from sources west of the Continental Divide in the North-Pacific and Northern Rocky Mountain regions have long, slender, flexible needles with slight to moderate thickening of the hypoderm cell walls, prevailingly in three-needle fascicles (fig. 14, *A*). Trees from east of the Continental Divide and in Colorado and Utah have foliage prevailingly in two-needle fascicles with short, thick, stiff needles with extremely thick hypoderm tissues (fig. 14, *B*) Trees from the Arizona-New

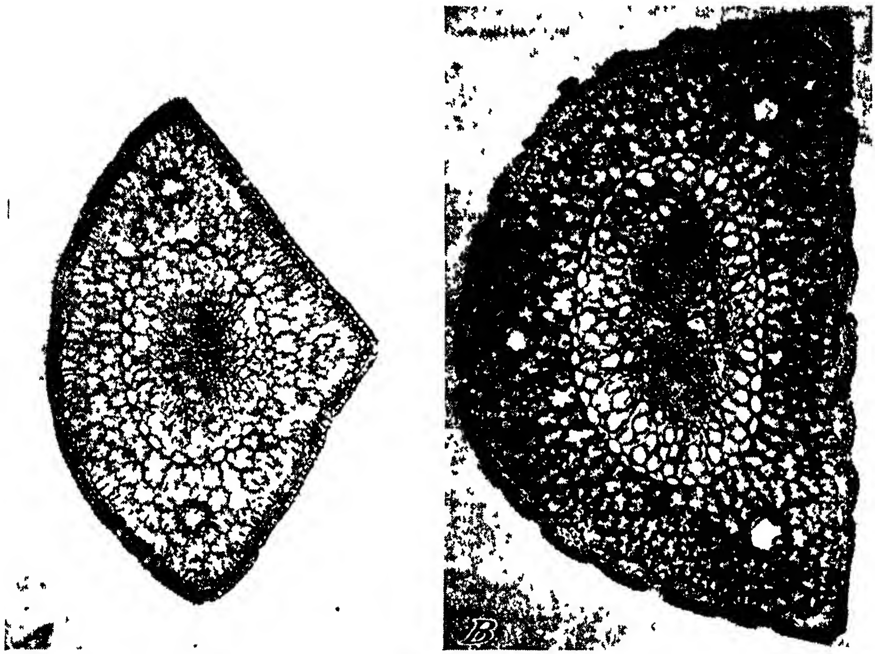

Figure 14.—Races of ponderosa pine show inherent differences in needle structure: *A*, An example of the thin hypoderm layer and lack of stomatal depressions of the long-needle type shown in figure 13, *A*; *B*, thicker hypoderm layer without stomatal depressions, characteristic of the short-needle type illustrated in figure 13, *B*.

Mexico Plateau have preponderantly three-needle fascicles, with moderate length and slenderness of needles, but with thick hypoderm structure. As these pronounced differences in foliage were found to be the same in trees of the parent localities, the conclusion is that these characteristics are strongly heritable.

Progenies that originated in localities within the northern Rocky Mountains, where the climate was similar to that of the experimental site, have made the greatest growth in height and diameter. Those from regions of more severe climates in Colorado, Utah, Arizona, and New Mexico have made the least. The slowest growing progenies in the experiment have reached an average height and diameter only half that of the fastest growing offspring. Comparison of progenies with trees growing in parent localities shows strong inheritance of growth rate in the new environment, except that the tendency is less marked where the progeny came from a region of more favorable climate.

Relative degree of hardiness was revealed by a sudden steep drop in temperature of 57° F. on December 15, 1924. Two progenies from the mild Pacific coast region were practically eliminated. The progenies from regions of the most rigorous winter climates suffered little or no loss by this freeze.

The results to date indicate that the most suitable seed source for planting in northern Idaho is from Republic, Wash., to the Continental Divide and from the Salmon River to the Canadian boundary. Introductions from the mild climate of the Pacific coast are subject to loss from sudden and severe temperature changes, which may occur periodically in Idaho. Although an introduced tree may be perfectly adaptable to the climate, it may, because of slow growth, be decidedly unsuitable for timber growing in northern Idaho. On this basis seed from Black Hills and southeastern Montana sources would be unsatisfactory, and Colorado seed would prove decidedly so.

Pacific Northwest Forest Experiment Station [14]

1. SEED ORIGIN

Pseudotsuga taxifolia (Douglas fir)

Five replicative plantations were established in 1915 with seed from 13 localities (northwestern Washington to central-western Oregon, 100- to 3,850-foot elevations) to study climatic and geographic races within the Pacific coast form. Progenies from individual trees representing variations in age, form, infection by wood-rot fungi, and site conditions were planted under separate pedigree numbers. No gross differences have been observed in morphological characteristics (leaves, crown, stem, flowers) between progenies from different seed sources. A significant and constant difference was observed in the relative time at which the various progenies burst their buds in the spring. Different progenies also varied in their susceptibility to late-spring frost injury. The progenies of certain individual parents were significantly taller than those from other parents growing in the same locality. The progeny from two of the seed-source localities made outstandingly good height growth on every plantation.

Pinus ponderosa (ponderosa pine)

Plantations were established in 1926 for a study of geographical races of this species. Results indicate that local stock is doing best in growth and survival. Progenies from different seed sources are already beginning to show rather distinct variations in the appearance of the foliage.

Rocky Mountain Forest and Range Experiment Station [15]

1. SEED ORIGIN

Pinus ponderosa (ponderosa pine)

Test plantations were established at Fremont in 1915 and 1916 with seed from seven sources (five Colorado, one Wyoming, and one South Dakota). Altitude range of seed sources was from 5,200 to 9,000 feet. A second test plantation was established in 1920 with seed from eight sources (one each from Montana, Arizona, California, Oregon, South Dakota, and three from Colorado). Data are available on survival, height, and form. The results from the standpoint of survival, rate of growth, and winter-hardiness point conclusively to the futility of using any but Colorado (not including southwestern pine type) and possibly Black Hills seed.

Test plantations were established in the Nebraska National Forest (1926) with seed from eight sources (Nebraska, South Dakota, Colorado, Arizona, New Mexico). The results indicate the superiority of local Nebraska seed. Southwestern and central Rocky Mountain stocks have been extremely susceptible to tip-moth attack. A segregated seed area has been established.

Pinus contorta (lodgepole pine)

A plantation at Fremont now 21 years old includes trees from seed collected from nine localities in Wyoming and Colorado. There is also a 17-year-old plantation, established with stock from 14 sources from approximately the same general region. In general the nearest seed sources have given the best results, but the extent of variation within a seed progeny largely eliminates the significance of the group performance.

A test planting in the Medicine Bow Forest, Wyo., is now 17 years old; seed from three sources (local, southern Wyoming, western Colorado). The relative survival and performance have been in inverse ratio to proximity of the seed source to the experimental area.

[14] At Portland, Oreg.
[15] At Fort Collins, Colo.

Pseudotsuga taxifolia (Douglas fir)

A 20-year-old plantation at Fremont includes stock from 11 national forests (6 in Colorado, 5 in Wyoming) and 15 climatic sources. Last observations (1923) indicate that local stock is decidedly superior in survival and height growth. Wyoming stock failed completely.

Picea engelmanni (Engelmann spruce)

A plantation on the east slope of Pike's Peak (elevation 10,500 feet), 24 years old, contains 10 climatic strains from 6 Colorado National Forest seed sources. Results are not conclusive.

2. Individual Seed-Tree Progeny Tests.

Pinus ponderosa (ponderosa pine)

Test plots were established in 1932 at elevations of 7,200 feet and 9,100 feet in the Pike's Peak locality with progeny from eight individual parent trees representing a 2,000-foot altitudinal range within the same locality. The lower plantation was eliminated by drought. In the upper plantation survival shows a fairly regular increase from low to high elevation sources.

Progeny from individual mistletoe-susceptible and presumably mistletoe-resistant trees are being tested in two 4-year-old plantations at Fremont station.

Three plantations (3, 4, and 6 years old) in the Nebraska sand hills include progeny of individual trees selected because of superior development and freedom from Peridermium.

Pseudotsuga taxifolia (Douglas fir)

Progeny of individual parent trees possessing peculiar branching habits are under observation in two plantations at Freemont (6 and 8 years old).

3. Tree Breeding

Artificial crosses between individuals of an apparently mistletoe-immune strain of *Pinus ponderosa* (ponderosa pine) have been successful. Seedlings are now 4 years old.

Southern Forest Experiment Station [16]

1. Seed Origin

Pinus taeda (loblolly pine)

Test plots were established in 1927 at Bogalusa, La., with trees from seed collected in Louisiana, Texas, Arkansas, and Georgia. Observation in the spring of 1936 (trees 9 years in field) showed local Louisiana seed definitely superior in growth rate. Other significant differences may exist.

Pinus palustris (longleaf pine), *P. caribaea* (slash pine), *P. taeda* (loblolly pine), *P. echinata* (shortleaf pine)

Test plantations were started on the Palustris Experimental Forest (1935–36) with stock from seed of various geographic sources. The following species were used: *P. palustris* (eight sources), *P. caribaea* (nine sources), *P. taeda* (two sources), *P. echinata* (two sources).

Seed of the following four species was obtained from 40 different sources in 1935: *P. palustris* (11 sources), *P. caribaea* (7 sources), *P. taeda* (12 sources). *P. echinata* (10 sources). Seedlings from seed of practically all sources for each species were grown at or near each point of origin, for planting during the 1936–37 planting season. The purpose of this is to test every geographic strain both in its own locality and in every other locality included in the study of that species. In at least one nursery distinct differences in size and in rate of maturing were apparent in the fall of 1936, the most conspicuous being between shortleaf pine seedlings from Pennsylvania and from Texas seed.

2. Individual Seed-Tree Progeny Tests

Pinus palustris (longleaf pine)

A test plantation was started in 1936 with 300 seedlings from parents high in naval stores yield and from parents low in yield.

[16] At New Orleans, La.

3. Tree Breeding

Pinus palustris x *P. caribaea*, hybridized in 1929, produced approximately 24 hybrid seedlings intermediate between the parents in stem, foliage, and bud characteristics, growth habit, and rate of growth. X *P. sondereggeri* (F_1) was crossed with *P. palustris*, *P. taeda*, and X *P. sondereggeri*. A few seedlings were obtained from each of these crosses and were planted out in 1933.

Southwestern Forest and Range Experiment Station [17]

1. Seed Origin

Pinus ponderosa (ponderosa pine)

Tests of climatic races are under way at the Fort Valley station. Results indicate that seed from California and the northwest portions of the United States invariably germinate less rapidly and produce larger, more succulent, but noticeably less hardy seedlings than local seed. Seed from Colorado, Utah, and Black Hills produce plants much like those from local seed, but Black Hills seedlings always show characteristic differences in color and form, and 20 years after planting are beginning to show signs of decline.

Tennessee Valley Authority, Forestry Division [18]

2. Individual Tree Selection

The tree crop unit of the Forestry Division has been interested in the selection of individual forest trees that combine desirable timber quality with production of high quality and quantity of fruit (nuts, acorns, berries). This work has been carried on through prize contests and through direct scouting. Up to the present time, one black walnut, two black locusts, two honey locusts, one ash, one hickory, and two oaks have been discovered which appear to merit special study. These individuals are being multiplied vegetatively by grafting and budding.

3. Tree Breeding

The tree crop unit initiated a project in hybridization and breeding in the spring of 1936. During this first year, a total of approximately 5,000 artificial pollinations were made with 72 species, varieties, and clones of the following 10 genera: *Juglans* (walnut), *Hicoria*, syn. *Carya* (hickory), *Corylus* (hazel), *Castanea* (chestnut), *Quercus* (oak), *Asimina* (pawpaw), *Amelanchier* (serviceberry), *Gleditsia* (honeylocust), *Robinia* (black locust), and *Diospyros* (persimmon).

The purpose of this breeding work was to produce trees combining high productivity and high quality of fruit (nuts, berries, acorns, pods) with desirable timber qualities. Such superior trees are needed for tree-crop planting and will, before maturity of the timber crop, pay their way by the annual production of food for man, stock, or game.

The severe spring drought in eastern Tennessee resulted in the loss of a considerable portion of seed that had originally set to cross-pollination.

United States— State, Private, and Endowed Agencies

Brooklyn Botanic Garden [19]

3. Tree Breeding

Controlled breeding experiments were undertaken in 1930, to produce a chestnut with inherently good timber form and high resistance to or immunity from the chestnut blight disease. The work was started with Japanese and American chestnuts, but in recent years additional species, varieties, and hybrids have been used as parent stocks. Some of these hybrids are now 5 years old. Up to the present time, the following *Castanea* hybrids have been produced ((R) indicates reciprocal crosses between the parents):

C. crenata (Japanese c.) × *C. dentata* (American c.)
C. mollissima (Chinese c.) × *C. dentata* (R)
C. S8 × *C. dentata* (R)
C. S8 × *C. crenata* (R)
C. crenata × (*C. crenata* × *C. dentata*) (R)

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[17] At Tucson, Ariz.
[18] At Norris, Tenn.
[19] At Brooklyn, N. Y.

(*C. crenata* × *C. dentata*) × *C. mollissima* (R)
(*C. mollissima* × *C. pumila* (chinquapin) × *C. dentata*
C. crenata × *C. seguinii* (Chinese chinquapin)
C. mollissima × *C. seguinii*
(*C. crenata* × *C. dentata*) × *C. dentata*
(*C. crenata* × *C. dentata*) × (*C. crenata* × *C. dentata*)

(NOTE.—S8 is apparently a combination of *C. crenata* and *C. pumila;* made by Walter Van Fleet, U S. Department of Agriculture.)

Many of the *C. crenata* × *C. dentata* hybrids give promise of timber types and appear to be resistant to chestnut blight. So far, they have been subjected only to natural infection, but in 1936 all hybrids were artificially inoculated. It is too early to determine the results of these inoculation tests. Some of the hybrids bloomed at 3 years of age; these were immediately used for further hybridization.

Fox Research Forest [20]

1. SEED ORIGIN

Investigations originally started by the Brown Co. are being conducted with Scotch pine, Norway spruce, and European larch. The purpose of these experimental plantations is to determine the most desirable proveniences for reforestation in New Hampshire. Most of the plantations are too young to provide pertinent information.

New York State Conservation Department, Bureau of Investigation [21]

1. SEED ORIGIN

Pinus sylvestris (Scotch pine)

Four generations, ranging in age up to 30 years, are now available for study. Observations to date indicate the possibility of rust-resistant strains and two apparently inherent growth forms; a straight-boiled, small-limbed type with small pointed crown, and a fairly straight-boled, large-limbed type with large bushy crown.

New York State College of Forestry [22]

2. SEED ORIGIN

Investigations with climatic varieties of two species of *Picea*, five species of *Pinus*, and two species of *Larix* have been started on the Pack Demonstration Forest, Warrensburg, N. Y.

Oxford Paper Co. in Cooperation with the New York Botanical Garden [23]

3. TREE BREEDING

A breeding project was initiated in the spring of 1924 to develop new hybrid poplars of particular value for pulpwood reforestation in Maine (Stout and Schreiner, 1933).[24] A total of approximately 13,000 hybrid seedlings was obtained from 99 different cross combinations between 34 different types of *Populus*, as follows:
The parents are arranged in alphabetical order within the main groups of poplars, and the extent to which each was used in hybridization is indicated by the use of the numbers assigned in the sequence. The number of seedlings grown for each cross is indicated in italics under the female parent. Thus in the cross *P. alba* × *P. alba nivea* 67 seedlings were grown.

A. The white poplars.
  1. *Populus alba* ♀ ×2 (*67*); 3 (*8*); 4 (*34*); 6 (*22*); 7 (*16*).
  2. *P. alba nivea* ♂ ×1.
  3. *P. canescens* ♂ ×1.

B. The aspens.
  4. *P. adenopoda* ♂ ×1, 17.
  5. *P. grandidentata* ♂ ×10, 31, 32.
  6. *P. tremula* ♂ ×1, 8.
  7. *P. tremula Davidiana* ♂ ×1.
  8. *P. tremuloides* ♀ ×6 (*11*).

[20] At Hillsboro, N. H.
[21] At Albany, N. Y.
[22] At Syracuse, N. Y.
[23] At Rumford, Maine, and Bronx Park, New York City, respectively.
[24] See Bibliography, published in the Yearbook separate of this article.

C. The black poplars and cottonwoods.

9. *P. angulata* ♀ ×10 (*583*); 11 (*248*); 12 (*99*); 16 (*203*); 21 (*214*); 22 (*60*); 25 (*214*); 26 (*205*); 34 (*264*).
10. *P. balsamifera virginiana* ♀ ×5 (*178*); 10 (*138*); 11 (*18*); 12 (*189*); 16 (*208*); 21 (*183*); 22 (*7*); 25 (*216*); 26 (*245*); 34 (*705*). ♂ ×9, 10, 13, 15, 18, 19, 23, 31, 33.
11. Cottonwood (unidentified) ♂ ×9, 10, 13, 15, 18, 19, 31.
12. *P. caudina* ♂ ×9, 10, 13, 18, 26, 29, 30, 31, 32.
13. *P. charkowiensis* ♀ ×10 (*288*); 11 (*267*); 12 (*266*); 16 (*263*); 21 (*312*); 22 (*52*); 25 (*188*); 26 (*249*); 34 (*221*).
14. *P. Eugenei* clone ♂ ×17, 23.
15. *P. fremonti* ♀ ×10 (*7*); 11 (*9*); 16 (*108*); 21 (*194*); 25 (*217*); 26 (*69*); 34 (*125*).
16. *P. incrassata* ♂ ×9, 10, 13, 15, 18, 19, 29, 31, 32.
17. *P. nigra* ♀ ×17 (*6*); 14 (*49*); 17 (*184*); 20 (*44*); 27 (*217*); 28 (*377*); 32 (*2*); 34 (*200*).
18. *P. nigra baatanicorum vitrum* ♀ ×10 (*6*); 11 (*60*); 12 (*51*); 16 (*10*); 21 (*157*); 25 (*170*); 34 (*121*).
19. *P. nigra betulifolia* ♀ ×10 (*11*); 11 (*11*); 16 (*141*); 21 (*65*); 25 (*166*); 34 (*209*).
20. *P. nigra Italica* (clon Lombardy) ♂ ×17, 23.
21. *P. nigra plantierensis* ♂ ×9, 10, 13, 15, 18, 19, 26, 29, 31, 32, 33.
22. *P. robusta* clone ♂ ×9, 10, 13, 32.
23. *P. sargentii* ♀ ×10 (*72*); 14 (*50*); 20 (*25*); 23 (*35*); 26 (*149*); 27 (*309*); 28 (*51*); 32 (*14*); 34 (*233*).
24. *P. serotina* clone ♂ ×26.
25. *P. volga* clone ♂ ×9, 10, 13, 15, 18, 19, 26, 31, 32.

D. The balsam poplars, and the older hybrids strongly balsam in character.

26. *P. barolinensis* ♀ ×12 (*8*); 21 (*17*); 24 (*29*); 25(*62*); 26 (*31*); 34 (*27*). ♂ ×9, 10, 13, 15, 26, 23, 29, 31, 32, 33.
27. *P. berolinensis rossica* ♂ ×17, 23.
28. *P. laurifolia* ♂ ×17, 23, 33.
29. *P. maximowiczii* ♀ ×12 (*179*); 16 (*2*); 21 (*145*); 26 (*112*); 34 (*5*).
30. *P. petrowiskyana* ♀ ×12 (*25*).
31. *P. rasumowskyana* ♀ ×5 (*2*); 10 (*56*); 11 (*30*); 12 (*70*); 16 (*25*); 21 (*76*); 25 (*81*); 26 (*183*); 34 (*148*).
32. *P. simonii* ♀ ×5 (*32*); 12 (*99*); 16 (*75*) 21 (*176*); 22 (*1*); 25 (*155*); 26 (*189*); 34 (*44*). ♂ ×17, 23.
33. *P. tacamahacca candicans* clone Balm of Gilead ♀ ×10 (*6*); 21 (*40*); 26 (*82*); 28 (*6*).
34. *P. trichocarpa* ♂ ×9, 10, 13, 15, 17, 18, 19, 23, 26, 29, 31, 32.

Approximately 700 hybrid seedlings were originally selected for intensive study and evaluation, and of this number 69 are still under close observation. Descriptions have been published of 10 of these hybrids that appear particularly promising for use in reforestation.

Propagation of the new poplar hybrids has been entirely vegetative, by cuttings. Many of the hybrids have so far indicated greater growth vigor than any previously known poplar species or hybrids. Some have been practically immune to certain diseases, particularly *Melampsora* rust and *Fusicladium* twig disease. Selections have included frost-hardy types with good forest form that grow vigorously from cuttings. There is evidence that the wood of many of the fast-growing hybrids will be denser, and will produce somewhat longer fibers, than the aspens now used for pulpwood. Most of the original hybrids are growing in plantations (now 9 and 10 years old) and many have begun to bloom; some individuals flowered at the age of 7 years.

Foreign Agencies

Austria, Forstliche Bundes, Versuchsanstalt, Mariabrunn

1. Seed Origin

Considerable research has been carried out on climatic races and on the importance of the seed origin of forest trees. This work was started previous to 1900. The progress of the work has been reported in publications by Cieslar, Tschermak, and Oehm.

Canada, Petawawa Forest Experiment Station,[25] *Ontario*

3. TREE BREEDING

Crosses between black spruce and Norway spruce, attempted in Canada in 1934, were unsuccessful. In 1936 *Populus canescens* was crossed with *P. grandidentata*, and *P. tremuloides* was crossed with *P. grandidentata*, in an effort to obtain a hybrid combining the wood characteristics required for match and veneer wood with resistance to heart rot.

C. Heimburger of this station reports that in 1932 he crossed red spruce with Norway spruce while working in New York State. Good seed was produced, and the seedlings are now being grown by the New York State College of Forestry.

Denmark, Royal Veterinary and Agricultural College, Copenhagen

3. TREE BREEDING

In the spring of 1924, *Abies concolor lowiana* (Pacific white fir) was successfully crossed with *A. grandis* (lowland white fir), and the hybrids are under observation at the present time. In 1929 *Juglans sieboldiana* (Japanese walnut) was successfully crossed with *J. cinerea* (butternut). Reciprocal crosses have been made between *Larix leptolepis* (Japanese larch) and *L. decidua* (European larch). Rather extensive self-pollinations have been made by covering portions of large trees, or entire smaller trees, with closely woven canvas. A tree of *Chamaecyparis* sp. was selfed by covering its top. A larch (7.1 m tall) thought to be a hybrid between *Larix gmelini* and *L. leptolepis* was tented and self-fertilized. A small Japanese larch was also selfed by potting and transferring it to a greenhouse.

Germany, Botanisches Institut der Forstlichen Hochschule, Eberswalde

1. SEED ORIGIN

Studies are now under way on climatic races of *Pinus sylvestris* (Scotch pine) and *Pseudotsuga taxifolia* (Douglas fir). Progenies of Douglas fir from 19 different seed sources are growing in the vicinity of Eberswalde. Particular emphasis has been placed upon the possible selection of Douglas fir races that are highly resistant to *Rhabdocline* leaf disease. Results to date indicate that in general the American coastal forms, although not entirely immune, are sufficiently resistant to warrant further use in forest planting; that the mountain forms are slower growing, more susceptible to the disease, and cannot be recommended; and that certain types should be discontinued entirely.

3. TREE BREEDING

Reciprocal crosses between *Pinus montana* and *P. sylvestris* have apparently been unsuccessful. Since natural hybrids between these species have been reported, it is possible that the negative results may have been due to lack of "crossibility" of the strains that were used.

Germany, Forstbotanisches Institut, Technischen Hochschule, Dresden (Forstliche Abteilung Tharandt)

1. SEED ORIGIN

Seed origin investigations of a large number of forest trees, including pine, spruce, larch, oak, beech, aspen, alder, ash, and maple, are under way at this station. In addition to the above the following species of most diverse seed origin are also being tested in experimental plots: *Pseudotsuga taxifolia, Betula verrucosa, Pinus murrayana, Abies cilicica, Pinus armeniaca, P. peuce. Picea engelmannii, P. sitchensis, Chamaecyparis lawsoniana.*

Great Britain, Forestry Commission of Great Britain, Research Division[26]

1. SEED ORIGIN

Investigations on climatic races of *Pseudotsuga taxifolia*, two species each of *Larix*, *Picea*, and *Quercus*, and four species of *Pinus* are under way. This work was started in 1925 and it is too early to draw any conclusions. The investigations will include a study of growth and form, frost-hardiness, and resistance to fungus and insect attacks.

[25] At Petawawa, Ontario.
[26] At London.

Switzerland, Eidgenössische Zentralanstalt für das Forstliche Versuchswesen, Zürich

1. Seed Origin

Studies on site races, form races, and so forth, were started in 1898 with two species each of *Pinus* and *Quercus*, one species each of *Picea, Abies, Larix, Fagus, Acer,* and other important tree species. These studies include the influence of geographical location, latitude, altitude, soil, precipitation, form, age, and position of the parent tree in the stand. Results indicate that the following characteristics are inherited: Color and size of needles and leaves, crown form, stem form, increment, growth periods, and resistance to frost, heat, light, snow, fungi, and insects.

These investigations are of great importance since they are to be applied to protection forests in many of the regions where natural regeneration is practiced. Results have been published by Engler, Nageli, and Burger.

BIBLIOGRAPHY

A bibliography for this article, including over 300 references related to forest tree breeding, will be published in the 1937 Yearbook Separate containing the text of the article.

BREEDING PROBLEMS WITH ANGORA GOATS

W. V. LAMBERT, Senior Animal Husbandman, Animal Husbandry Division, Bureau of Animal Industry

SINCE its domestication the goat has served man well. As a source of milk, meat, mohair, and skins it has furnished him both food and clothing, and because of its brush-eating proclivities, has spared him untold amounts of hard labor with the brush hook.

Since 1900 the Angora goat industry in the United States has undergone rapid expansion. At present it is confined largely to the Southwestern States, nearly 90 percent of all Angoras being produced in Texas, New Mexico, and Arizona. The estimated average yield of mohair per goat in 1935 was 4.4 pounds although the average yield in some of the better flocks was probably twice as great. Practically all improvement has come about through practical breeding. In comparison with other farm animals, little in the way of scientific research has been done with the Angora goat. The Texas Agricultural Experiment Station is the only place in the United States where experimental work is now known to be conducted with this breed. Research is badly needed on problems pertaining to the development of strains yielding larger amounts and a better quality of mohair. Techniques have been developed for the study of mohair that, combined with the proper genetic research, offer possiblities of improvement yet unrealized.

It is quite certain that the goat was one of the first domestic animals. In all probability, it was first domesticated in western Asia, and from there it was brought into Africa and other countries. After centuries of selection, the domestic goat is very different from its wild ancestor.

The goat is probably descended from the pasang or Grecian ibex (*Capra hircus aegagrus*), a species of wild goat found in Asia Minor, Persia, and contiguous countries. It appears unlikely that any wild species other than the pasang had an appreciable part in the ancestry of the domesticated goat, although for some breeds, as the Malayan, Cashmere, and Angora goats, the evidence is not so convincing that this form was the sole ancestor. It is possible that the ibex and markhor may have been represented in the ancestry of these breeds, for Lydekker (*9*)[1] states that both of these forms will breed readily in confinement with domesticated goats.

The development of the long-haired type of goats was accomplished centuries ago, principally in Asia Minor, where the Province of Angora gave its name to the best known of such breeds. How the short hair of the pasang and other possible ancestral forms developed

[1] Italic numbers in parentheses refer to the Bibliography p. 1292.

into the long hair characteristic of the Angora goat is not clear, but it seems most likely that it was simply by the selection of animals with variations in length of hair. Whether a single major mutation accounted for the change, as appears probable for long-haired types in the rabbit and the guinea pig, is unknown, but it would seem certain that the selection of minor variations in length of hair has modified the character in the desired direction.

According to Willingmyre, Window, Spencer, and others (*20*), the original Angora goat was described as a comparatively small animal with a fine lustrous, silky fleece that hung in ringlets and attained a length of 8 to 10 inches. In the early part of the nineteenth century the demand for raw mohair became so great that the Turks, who were the original breeders of the Angora, were unable to increase their herds rapidly enough to meet the demand. This resulted in hybridization of Angora bucks with common Kurd does in an effort to increase the number of mohair-producing animals quickly by grading up the common goats of the region. This practice became so prevalent that purebred Angora goats were practically eliminated. However, the new type of Angora developed from these cross-breds is a larger and hardier animal that yields a heavier though somewhat coarser fleece than the original Angora.

THE DISTRIBUTION OF ANGORA GOATS FROM ASIA MINOR

ALTHOUGH the Angora goat was developed in Asia Minor centuries ago,[2] its spread into other portions of the world is relatively quite recent. The first European record of the Angora goat appears in 1554 when, according to Cronwright Schreiner (*2*), the Dutch ambassador at Constantinople procured a pair of Angoras and sent them to the Emperor, Charles V. However, mohair yarn was known before this date in Europe. Following this early importation of Angora goats

[2]The use of mohair can be traced to the time of Moses. The Bible records that Moses commanded the children of Israel, after being delivered from slavery in Egypt, to bring white silk and goats' wool to weave altar cloths for the tabernacle (*20*).

ONE *of the most urgent needs for breed improvement in all branches of livestock, including mohair goats, is the development of more and better criteria for the selection of breeding animals. Too generally, selection is based solely upon the animal's appearance, or phenotype, and it is a well-known fact, substantiated both by practical experience and by genetic evidence, that appearance is not always a good criterion of an animal's breeding worth. It is of value and must be taken into account, but it is only a part of the story. The question is, not what an animal looks like, but what inheritance it will pass on; and it is impossible to determine this from appearance.*

to Europe, many attempts were made to establish them but without success until the nineteenth century.

In 1838 Angora goats were first introduced into South Africa. These goats were crossed with native goats and by a process of selection and inbreeding, herds of high merit were established. The goats were prized by the Boers, not so much for their mohair, but, according to Rose (*12*), because the infusion of the Angora blood into the native herds made the cross-bred goats less subject to cutaneous diseases and more able to resist scab. The cross-breds were also earlier maturing and heavier than the native goats, and their flesh was more palatable. No more importations were made into South Africa until 1856, but after that date several were made and the industry has grown until today South Africa, Turkey, and the United States are the countries producing the largest quantities of mohair.

The first importation of Angoras into the United States was made in 1849 by James C. Davis of Columbia, S. C. It consisted of nine choice animals—seven does and two bucks. These goats were exhibited at many fairs, where they won numerous prizes and received much publicity, with the result that great interest was stimulated in Angora goats.

In 1860 a second importation of 8 Angoras was made by William Henry Stiles of Cartersville, Ga., this being followed by an importation of 67 goats by Winthrop W. Chenery of Belmont, Mass., in 1861. In the next decade several importations were made, including one by Israel S. Diehl, who had been commissioned by the United States Commissioner of Agriculture in 1867 to visit the Province of Angora for the purpose of investigating the mohair industry.

During the 30 years from 1870 to 1900 several small importations were made by various breeders, mostly bucks to be used in the importers' herds. In 1904 one of the largest and most notable of all importations, consisting of 148 goats, was made by G. A. Hoerle of Midland Park, N. J. This shipment, which came from South Africa, was made possible by the temporary suspension during the Boer War of the very high export duty of 100 pounds sterling on each Angora goat by the South African Government. Soon thereafter the exportation of Angora goats was prohibited from South Africa and this embargo remained in effect for nearly 20 years.

Recent importations of Angora goats have been few and limited to a small number of individuals, mostly bucks. The latest importation from South Africa was made by E. Cawood into Texas in 1925.

THE ANGORA GOAT INDUSTRY IN THE UNITED STATES

FOLLOWING the Civil War the growing of Angora goats spread into many parts of the country and the number of goats increased rapidly. Introduction into new regions was at first largely for the purpose of brush extermination on new lands being opened for settlement in the West. In some regions where these goats proved to be well adapted, however, an interest in Angoras for the production of mohair developed, and the industry has finally become firmly established in certain sections.

Since 1900 the industry in the United States has undergone rapid expansion. The number of Angora goats increased from 329,300 in

1900 (*1*) to 2,101,591 in 1920 and to 3,785,127 in 1930 (*14*). Figures showing the status of the Angora goat industry in the United States in 1930 are given in table 1.

TABLE 1.—*The status of the Angora goat industry in the United States in 1930*

Region	Total Angora goats	Angora goats by regions	Total farms in the United States	Farms reporting Angora goats		Average per farm reporting
	Number	*Percent*	*Number*	*Number*	*Percent*	*Number*
Texas	2,956,584	78.1	495,489	9,287	1.9	318.4
New Mexico	193,639	5.1	31,404	1,177	3.7	164.5
Arizona	193,320	5.1	14,173	590	4.2	327.7
Oregon	119,341	3.2	55,153	2,895	5.2	41.2
Missouri	78,839	2.1	255,940	3,454	1.3	22.8
California	45,286	1.2	135,676	1,025	.8	44.2
All other States	198,118	5.2	5,300,813	15,951	.3	12.4
United States	3,785,127	100.0	6,288,648	34,379	.5	110.1

From these figures it is apparent that Angora goat production is largely confined to the southwestern part of the United States; and that Texas had over 78 percent of all Angora goats in 1930, with New Mexico and Arizona accounting for over 10 percent of the remaining goats. In Texas the majority of the goats are raised in the Edwards Plateau area in the southwestern part of the State, where they are kept in large numbers on ranches. In Arizona and New Mexico similar conditions exist, this method of production being responsible for the large number of goats reported per farm in those States.

Since 1930 there has been some decline in the total number of Angora goats in common with a reduction in number for most classes of livestock. The 1935 census of agriculture listed 4,093,441 goats of all kinds in the United States, whereas in 1930 a total of 4,821,294 were listed. If there was a proportionate reduction in the number of milk and Angora goats the approximate number of Angora goats in the United States in 1935 was 3,211,000.

The production of mohair and estimated average weight of mohair fleeces at 5-year intervals since 1920 for the six leading States are shown in table 2. While the total production of mohair increased in proportion with the increase in number of goats, it may be noted that the average production per goat did not increase greatly, although there was a slight, but not constant, increase in average fleece weight. For some States, notably Texas, New Mexico, and Oregon, the average weight of fleece was greater than for other States. The reason for this is not apparent, but it is probable that both better breeding and better management were responsible. For instance, Angora goats in Missouri are kept in small herds principally for the purpose of clearing brushland, whereas in Texas and some of the other States they are kept in large herds primarily for the production of mohair. It is to be expected that in Texas more careful attention will be given to the selection of breeding stock, as well as to providing conditions most favorable for mohair production.

In addition to its value as a producer of mohair, which is a very important textile fiber, the Angora goat is useful for clearing brush

from virgin land (fig. 1 illustrates the feeding habits of the animals) and it is a valuable source of meat. During the fiscal year ended June 30, 1936, a total of 51,461 goats were slaughtered in packing plants under Federal inspection (*13, p. 27*), a large proportion of which were

Figure 1.—Angora goats browsing. This is a common scene in the Edwards Plateau section of Texas. The goats obtain a large part of their feed from the browse that grows abundantly in this section.

Angora goats. This meat, sometimes known as chevon, is similar in flavor to lamb and mutton.

Table 2.—*Production of mohair (including kid hair) and estimated average weight of mohair fleeces per goat in the 6 leading producing States at 5-year intervals from 1920 to 1935, inclusive*

State	1920		1925		1930		1935	
	Production	Fleece weight	Production	Fleece weight	Production	Fleece weight	Production	Fleece weight
	1,000 pounds	*Pounds*	*1,000 pounds*	*Pounds*	*1,000 pounds*	*Pounds*	*1,000 pounds*	*Pounds*
Texas	6,786	3.7	8,519	4.6	14,800	4.2	13,000	4.6
New Mexico	397	3.2	444	3.7	815	3.9	920	4.1
Arizona	464	3.2	599	3.7	900	4.0	480	3.2
Oregon	452	4.0	462	4.2	480	4.0	331	3.8
Missouri	145	2.5	188	2.8	168	2.5	210	2.5
California	230	3.6	220	4.4	140	3.5	133	3.8
Total or average	8,474	3.6	10,432	4.4	17,303	4.1	15,074	4.4

Bureau of Agricultural Economics, U. S. Dept. of Agr.

Goat meat, according to Williams (*19*), goes quite generally into the regular meat trade. In cities and towns in the range districts Angora wethers are marketed freely as such and the meat is consumed without discrimination by the buyer. According to some buyers properly finished goat meat has a sweetness lacking in mutton. Studies by Miller [3] indicate that the flavor of the meat from kids and lambs is very similar; in fact, the flavor was identical as far as the committee judging the two types of meat could decide. The goat meat was a little coarser in texture and for the older goats was graded as slightly tougher and somewhat drier. In eastern markets the status of goat meat has never been established and occasional efforts to sell it in these markets have been disappointing.

In general the goat carcass is not so well-fleshed, it is not susceptible of so high a finish, nor is the dressing percentage so high as that of the average sheep carcass. The selling price of the Angora wether is about 60 percent of that of the sheep wether where large numbers are sold. The lower price of chevon meat is attractive to consumers, and the quality of the meat is probably superior to that of mutton that could be obtained for the same price (*19*).

Improvement Brought About by Selective Breeding

The improvement of Angora goats in the United States has come about through selective breeding. Following the early importations, imported bucks were used extensively on a foundation of common short-haired does. Through selection and the use of imported bucks improvement progressed until the supply of high-class stock is now so plentiful that cross-breeding is seldom practiced. At present the chief method of breed improvement is based on a program of selection within purebred Angora stocks. Figure 2 shows a buck and a doe representative of the breed.

For the most part, the range herds of Angoras are composed of high-grade does that are mated with purebred bucks obtained from breeders who specialize in the production of registered animals. Most of these breeders are in the States of Texas, Oregon, New Mexico, and Arizona.

Agencies That are Sponsoring Breed Improvement

In 1900 the American Angora Goat Breeders' Association established a registry system for Angora goats. The foundation animals admitted to registry were chosen after official inspection of high-grade American Angoras, and only animals conforming to the standards required by the association were admitted. From 1900 to 1924 all goats registered by this association traced to these foundation animals or to Angoras imported during this period. In 1918 another association, the National Angora Record Association, was organized and incorporated under the laws of Texas, but this association merged with the American Angora Goat Breeders' Association in 1924. At present the latter association is the only organization registering Angora goats in the United States. Up to 1937 a total of about 170,000 Angora goats have been registered. Claudine Bourland of Rock Springs, Tex., is the secretary of this association. The directory of the association, pub-

[3] Miller, R. H. Quality and palatability of chevon. Master's thesis, Oreg. State Col. 1929.

lished in October 1934, lists a total of 353 members, 266 of whom are in Texas.

Other organizations that are active in sponsoring Angora goat breeding and improvement are the Arizona Mohair Growers' Association and the Texas Sheep and Goat Raisers' Association.

The Angora Journal, published at Portland, Oreg., by A. C. Gage, is the only journal in the United States that specializes exclusively

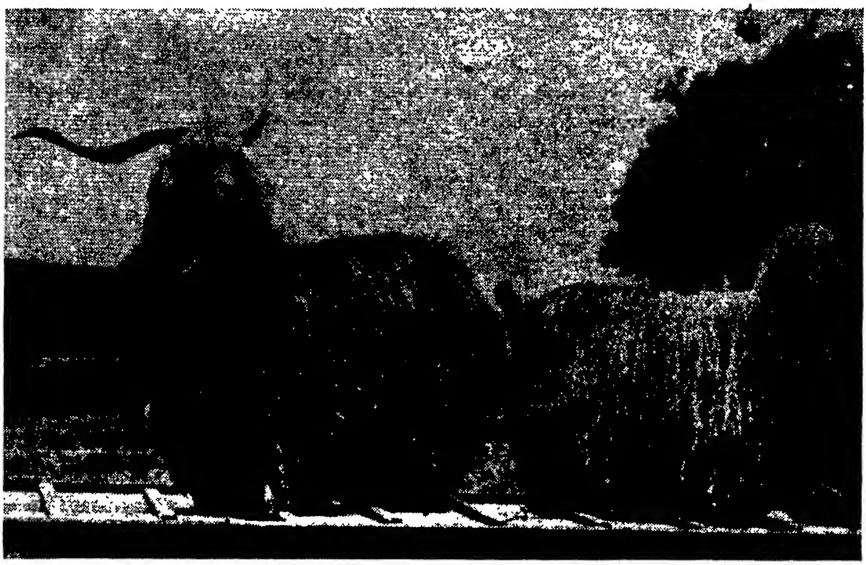

Figure 2.—An Angora buck and doe in full fleece. These individuals are good representatives of the breed.

on the promotion and improvement of Angora goats. The Southwestern Sheep and Goat Raisers' Magazine is the official publication of the Texas Sheep and Goat Raisers' Association.

RESEARCH, INCLUDING THAT AT FEDERAL AND STATE STATIONS

Research pertaining to Angora goats either by States or by the Federal Government is very limited. At present, only three projects are listed in the Office of Experiment Stations that deal with Angora goats, and these are all being conducted at the Texas Agricultural Experiment Station. They cover:

1. The inheritance of type in Angora goats.
2. Inheritance of the ridgling [4] characteristic in goats.
3. Cytological and hybridization studies with goats.

In 1915 the Texas Agricultural Experiment Station established a branch experiment station, generally known throughout the Southwest as the Ranch Experiment Station, in the Edwards Plateau section midway between Sonora and Rock Springs (fig. 3). Much

[4] Ridglings or "rigs" are animals characterized by cryptorchidism, the condition in which one or both testes fail to descend into the scrotum. Usually it involves but one testis, but occasionally both.

of the research at this station has been devoted to a study of Angora goats and mohair, and several bulletins have been published dealing with various aspects of mohair production, particularly studies on the influence of such factors as age, sex, individuality, and pregnancy upon the quantity and quality of mohair produced. The Bureau of Animal Industry of the United States Department of Agriculture has

Figure 3.—The laboratory building at the Texas branch experiment station near Sonora, Tex. This is the only research institute in the United States that is carrying on investigations with the Angora goat.

cooperated in some aspects of these investigations, chiefly on studies pertaining to quality of mohair.

Several years ago the Oregon Agricultural Experiment Station maintained an experimental herd of Angora goats, but with the curtailment of funds for research that followed the depression, this herd was disbanded.

Results of the Germ-Plasm Survey

As a part of the survey of germ plasm in animals and plants, the Department of Agriculture sent questionnaires to agricultural experiment stations in those States where Angora goats are of considerable economic importance and also to all prominent breeders whose names could be obtained. The breeder was asked for information concerning (1) the size of his herd, (2) the number of purebred and grade goats in the herd at present and during each of the last 5 years, (3) the total yield of mohair for each of the last 5 years, (4) the number of sires used in the herd, (5) the proportion of single and multiple births observed during the last 2 years, (6) the names of any outstanding strains bred by him, and (7) whether he was practicing inbreeding. If he was practicing inbreeding the breeder was requested to furnish pedigrees of several of his most highly inbred animals.

There were very few returns from the questionnaire, and as a result no very definite conclusions can be drawn. Some breeders

reported that they were practicing some inbreeding, but no pedigrees from which the degree of inbreeding could be determined were included in their replies. Nor is this information available anywhere in published form, since the record association does not publish herd-books. While a few breeders have attempted to develop and maintain certain breed lines, the number of attempts to do this is small and no families that could be compared with some strains of cattle—as, for instance, the Anxiety 4th Herefords—were reported. It is improbable that such strains exist among Angora goats. Some breeders follow the plan of using bucks produced in their own herds; others the plan of purchasing sires from other herds; while some use a combination of both plans. Since no importations have been made in recent years, little improvement has recently been accomplished in this manner. Apparently there has been a tendency among Angora breeders to breed for definite points such as certain fleece types, the elimination of beards, etc., rather than for the development of breed lines of especial merit.

From the data submitted it is apparent that mohair production in the flocks of the better breeders is much above the average reported in table 3. Two breeders reported an average annual production per goat during the last 5 years of over 7½ pounds; others, an average annual production of over 6 pounds. These figures are from 2 to 3 pounds, or some 40 to 70 percent, above the estimated average production for all Angora goats.

No great tendency was observed in any of the herds reported for the production of multiple births. A considerable reduction has been made in the size of some purebred flocks since 1930.

Genetic and Fleece Studies on the Angora Goat

Only a few investigators have studied the genetics of the Angora goat and most of the studies reported thus far are in their preliminary stages. Warwick (*16*) found that the presence of horns is dominant to hornlessness in the Angora and he suggests that one major factor governs the inheritance of this character, although the data are too few to allow for definite conclusions. Most purebred Angora goats have horns.

Cryptorchidism, an inherited defect that is quite common in Angora goats, has been investigated by Lush, Jones, and Dameron (*8*), and by Warwick (*15*). The exact mode of inheritance is not known, and its determination is difficult since the defect can be observed only in the male. The condition is recessive and at least two pairs of factors are involved.

The mode of inheritance of fleece length has not been determined, but Davies (*3*) states that the long-haired condition appears to be recessive. From the meager evidence available, however, it seems probable that hair length is determined by multiple factors.

The effect of individual differences and of such factors as age, sex, pregnancy, and lactation on the quality and quantity of fleeces produced by Angora goats has been investigated by Lush and Jones (*7*), and by Jones, Warwick, Dameron, and Davis (*6*). The studies by Lush and Jones show that about 17 percent of the differences in fleece weight produced by goats similar in age, sex, and general breed-

ing is permanent throughout the life of an individual and hence is subject to selection. The exceptional individual is of more importance in the less uniform flocks, and it is in such flocks that selection would be most effective. It was determined, furthermore, that permanent differences in fleece weight show up less accurately at first shearing than at later shearings and that they show more accurately at the fall yearling shearing, usually the second shearing, than at any other age. This is an important determination from the breeder's standpoint since culling at this age will result in the selection of those goats with the greatest inherent mohair production.

Jones, Warwick, Dameron, and Davis (*6*) found that the age of the animal had a marked influence on both the unscoured and the clean weight of the fleece, the weight increasing to a maximum at 3 years, after which it becomes steadily less. Diameter of mohair fiber and body weight were shown to increase until the animal reached 8 years of age. Length of staple, amount of kemp or coarse inferior hair in the fleece, and the extent of belly covering were somewhat less influenced by the age of the animal. Staple length reaches its maximum the first year and the mohair produced during the first year is of somewhat better quality than that produced later.

The body weight of bucks was found to be about 23 percent greater than that of does, while their fleece weights averaged about 18 percent greater unscoured and 29 percent greater when clean. The diameter of fiber was observed to be coarser in the fleece of the male but the staple length was somewhat less. Pregnancy was shown to reduce the fleece weight, as did the suckling of young. A somewhat similar effect of pregnancy was observed upon staple length although this effect is more pronounced in younger than in older animals.

Attempts to Cross the Sheep and Goat

Various investigators (*11*) have described apparent sheep-goat hybrids and a few writers have stated that such hybrids are rather common in some sections. Other workers have questioned these conclusions, and in the light of controlled attempts to make this cross it is probable that living hybrid offspring are rare, if they exist at all.

Heller, cited by Popenoe (*10*), reported that attempts to make such crosses between Barbados sheep and the goat in the laboratories of the Bureau of Animal Industry were unsuccessful. Recently Warwick, Berry, and Horlacher (*18*) described attempts to cross Angora does with rams, mostly of the Merino breed. In all 38 such matings were made. In 21 females it was determined that fertilization and implantation of the egg took place, but in no case were living young obtained. Two of these does were sacrificed, one 44 days after breeding and the other 62 days after mating. In both cases apparently normal embryos were found. The causes for the early death of the hybrid fetuses have not been determined.

Not all rams that were tried would mate with the does and, contrary to general opinion, Angora males would not mate with ewes. However, one Angora male that was raised on a sheep foster mother was mated with 17 ewes, but there is no evidence that fertilization occurred in any of these cases (*17*).

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OPPORTUNITIES FOR FURTHER IMPROVEMENT

It is apparent from the facts presented here that credit for improvement of Angora goats must go to private breeders, past and present, who alone have been responsible for bringing this breed to its present development. But improvement is now very slow, and if further progress is to be stimulated and encouraged, new measures are called for. On this point few will disagree, but the breeder may well ask what steps can be taken to bring about further improvement. It must be confessed that there is no single easy formula. If further improvement is desired, what will be needed is a program that includes the active cooperation of breeders, breed associations, State and county extension workers, and finally, the research staffs of State and Federal experiment stations.

No attempt will be made here to outline a research program for Angora improvement, but some of the points that need be considered will be briefly discussed.

One of the most urgent needs for breed improvement in all branches of livestock husbandry at the present time is the development of more and better criteria for the selection of breeding animals. Too generally, selection is based solely on the animal's appearance, or phenotype, and it is a well-known fact, substantiated both by practical experience and by genetic evidence, that appearance is not always a good criterion of an animal's breeding worth. It is of value and must be taken into account, but it is only part of the story. The question is, not what an animal looks like, but what inheritance it will pass on; and it is impossible to determine this from appearance. How to determine it is a question that science is as yet far from having answered in the case of animals. Research workers are attacking the problem, however, and eventually methods should be devised for determining and evaluating the factors of greatest importance in the selection of breeding stock.

Meanwhile, in spite of present uncertainties, it is known that the progeny test is important in evaluating breeding animals. To use the progeny test properly, however, requires the development of better records than those that now exist for mohair production. This is one part of an improvement program in which the practical breeder can cooperate to advantage with the scientist. Before such tests are undertaken, however, careful thought must be given to the kind of records that will be of the greatest use.

To use the progeny test most effectively the breeder must have accurate data on the offspring of his herd sires. Among the records of most importance are quality of mohair, freedom from kemp, uniformity of body covering, and yield of mohair determined on a clean basis. While facilities are probably not now available for securing all such information, records could undoubtedly be obtained if there were a sufficient demand for them. In addition to their value to the breeder in the selection of sires, such records would be of use to the scientist in getting at the basic physiological problems concerned in mohair production; and a more complete knowledge of such factors is essential to continued progress.

Very little information exists concerning the inheritance of any characters in the goat and particularly of those characters that are

concerned in the production of good fleeces. Research in this field is badly needed, since progress in breeding for fleece improvement must ultimately depend on a better understanding of the genetic factors involved. As an example, take the appearance of kemp in the fleece (fig. 4). The elimination of kemp fibers, which greatly reduce the value of the fleece, is one of the most important problems in Angora goat improvement. Until it is known how the kemp-producing characteristic is inherited, it can hardly be eliminated from herds.

There are now outstanding animals in the herds of many breeders, but along with them there are many mediocre and some inferior

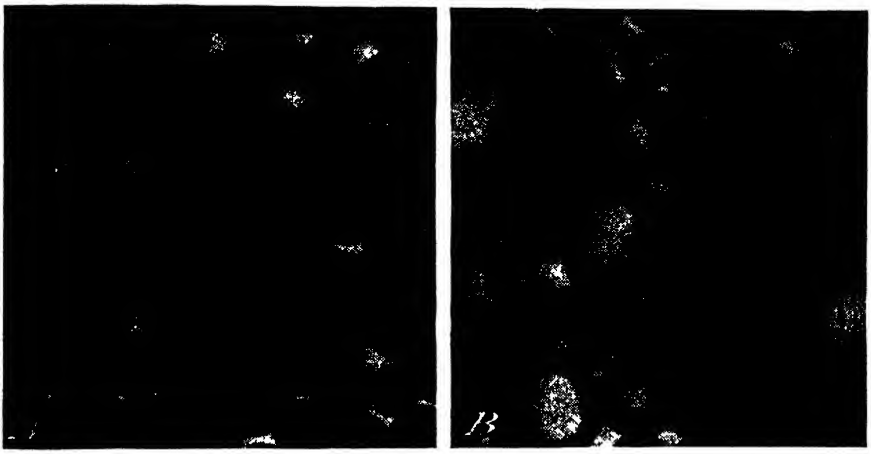

Figure 4.—Cross sections of mohair fibers showing (*A*) freedom from kemp and (*B*) the presence of many kempy fibers. The kempy fibers, which are short, coarse, and irregular, are characterized by a medullated or hollow central portion. They do not take dye readily, and because of this and their stiffness and poor spinning qualities, the presence of such fibers in a fleece lowers its value.

animals. If it were possible for the breeder to increase the uniformity of the animals in his flock it would be a decided step forward. Little is now known of the factors making for uniformity of fleece type, although this question is of vital concern to the breeder and the producer alike. Research that will lead to the development of methods for improving uniformity in flocks is badly needed.

These are two problems that should form part of a research program. Others might be discussed, but enough has been said to indicate the need for a scientific approach to the problem of improvement. Research commonly yields large returns for the funds and efforts expended, but the active encouragement of the industry is needed if an adequate research program for the improvement of Angora goats is to be carried on.

Some Immediate Practical Steps

In addition to sponsoring research Angora goat producers might foster improvement in other ways. One method that has particular merit would be the development of a system of recording based on

meritorious production of mohair similar to the register of merit for many breeds of dairy cattle. In such records scoured weight, fineness, and uniformity of fleece and freedom from kemp should be particularly stressed. Other steps that would be helpful would be the inclusion of more information in pedigrees than they now contain, with provision for certification of production records by some competent and impartial authority. Since Angora goat breeders are concentrated in a relatively few States, it should be possible to arrange for such certification of records with a minimum of cost to breeders. Such programs have been developed for register-of-merit records for other animals, and a similar scheme could be easily devised that would meet the requirements for breeders of Angora goats.

Again, if mohair were sold on a quality rather than on a weight basis it would exert an influence toward improvement in the breed by stimulating producers to raise better goats. This is worth serious effort on the part of the breeders and their record association. The adoption of different methods for the awarding of prizes at shows would also be a step to encourage better breeding practices. More emphasis should be placed on the get of sires and on outstanding families, and prizes should be awarded to breeders on this basis. This is in line with the progeny test, and it would focus the attention of breeders on the breeding ability of their choice animals.

Many difficulties beset those who undertake the improvement of modern breeds of livestock. But in spite of the excellence of modern breeds, their inherent variability is still great and the opportunities for improvement are many. The situation is a challenge to breeder and scientist alike, and if any great progress is to be made they must work closely together.

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IMPROVEMENT OF MILK GOATS

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ACCORDING to a recent survey by the United States Department of Agriculture, only two research institutes in the United States are now conducting investigations on milk goat breeding. Both institutions, the New Mexico Agricultural Experiment Station and the Department of Agriculture, have brought about great improvement in their herds by grading up common does with purebred bucks of milk breeds, and the results indicate great potentialities for milk goat improvement by the application of breeding methods.

THE GOAT AS A MILK PRODUCER

MILK goats are widely distributed in the United States but, in contrast with Angora goats, they are generally found in small herds and in many cases as one or a few individuals kept on the farm or in the back yard of the urban dweller. While they have not attained the position of economic importance of other classes of livestock, their numbers are increasing. Because a good milk goat will supply sufficient milk for the average family for at least 9 to 10 months of the year and can be kept where it would be impossible to keep a cow, they occupy a place in American agriculture not filled by any other class of livestock, and one that is probably destined to be increasingly important.

The average milk production is low, but there are many high-producing individuals and some herds in which the average milk production is high. Great variability exists both in rate and persistency of lactation.

The income of milk goat producers is derived principally from two sources—the sale of breeding stock and the sale of milk and milk products. Goats' milk has only a specialized demand and the development of goat dairy enterprises has been limited largely by the market created by the producer's own initiative. The producer of good breeding stock, on the contrary, has been in a more favorable position, for generally a greater demand exists for good stock than can be supplied.

Goat meat and goatskins also contribute to a limited extent to the income of the goat producer. Thousands of goats are slaughtered annually and their meat enters the same general channels of trade as mutton and lamb. Their skins are used in the manufacture of shoes, gloves, book bindings, pocketbooks, and other small articles. The number of skins produced annually in the United States is not large

and millions of skins are imported each year. From July 1934 to July 1935 a total of about 60 million pounds of skins were imported.

Breeds of Milk Goats in the United States

The goat is one of the most ancient of domestic animals. Most authorities agree that the numerous varieties are descended from the Persian wild goat, *Capra hircus aegagrus*, a species common in Asia Minor. Just when it was first introduced into Europe is unknown, but remains of goats are found among the ruins of early European races.

Records of early settlements in Virginia and New England indicate that goats of the milk type were brought to the United States by Capt. John Smith and by Lord Delaware. Goat raising, while of some consequence to the early settlers, gradually declined after the middle of the seventeenth century.

Serious attention began to be paid to the breeding of milk goats in the United States about 30 years ago. Prior to 1904 there were scarcely any purebred Swiss goats in the United States, records revealing but one importation, that of four head in 1893. In 1904 a consignment of 10 Saanen and 16 Toggenburg goats was brought in, and this was followed by several other importations during the next two decades. Animals from these importations were widely dispersed by sale throughout the United States, and have provided the basis for the development and improvement of milk goats in this country.

The important breeds of milk goats in the United States are those that have proved most popular on other continents—the Saanen, Toggenburg, Nubian, Maltese, and Alpine. Representatives of these breeds of improved milk goats, although increasing, are not so numerous in this country as the unimproved types of short-haired goats. Among them are large numbers of the common, or American, goat. A quarantine against the importation of goats from many countries largely accounts for the small number of breeds found in the United States.

A GOAT *can be kept where it would be impossible to keep a cow, and a good producer will supply sufficient milk for the average family. The milk is a wholesome and nutritious food, and in addition the meat is palatable and nutritious. In localities where an adequate supply of milk is not available and the keeping of cows is impracticable, good milk goats would contribute materially to the welfare of many families, especially those of low income. Thus there can be no doubt of the value of efforts to improve the milk production of these animals in the United States. However, the improvement of the milk goat, in common with that of other species of livestock, is a large task that requires the best efforts of the breeder, the research worker, and all other interested agencies.*

The Saanen and Toggenburg breeds of milk goats are the most popular in point of numbers in this country. Both breeds originated in Switzerland. Purebred Saanens (fig. 1, *A*) are solid white in color and large in size, mature males weighing 175 pounds or more and mature females, 125 pounds or more. The dairy conformation is especially well developed. The marked ability of this breed to produce milk is evidenced by the fact that the highest official test on record in the United States was made by a Saanen doe that produced 4,161.7 pounds of milk in 9 months and 10 days, an average for the period of 6.9 quarts a day.

The body color of Toggenburg goats (fig. 1, *B*) is brown or chocolate with a white stripe or bar down each side of the face, and the legs below the knees and hocks are white. Two wattles attached to the underside of the neck are very characteristic

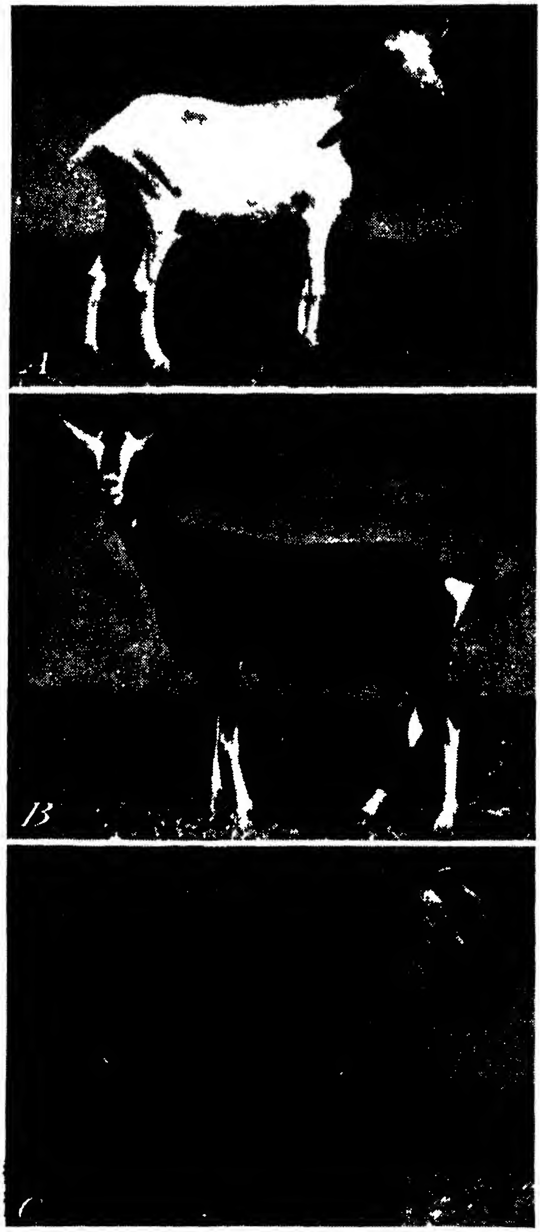

Figure 1.—High-producing does from three different breeds: *A*, Saanen; *B*, Toggenburg; *C*, Anglo-Nubian. The Saanen doe (No. 40728, Advanced Registry No. 191 A. M. G. R. A.) produced 3,144.4 pounds of milk and 95 pounds of fat in 10 months. Her highest daily yield was 17.6 pounds. The Toggenburg doe (No. 41642) produced 11 pounds of milk daily for a 30-day period as a 4-year old. Each one of these does came from high-producing ancestors and each has won high honors in the show ring. The Anglo-Nubian doe (No. 34278, Advanced Registry No. 201) produced under official test as an 8-year old an average of 12.1 pounds of milk, averaging 5.7 percent fat, daily for 3 months.

of this breed. Does of this breed, while not usually producing as large quantities of milk as those of the Saanen breed, are excellent milkers and a Toggenburg doe has made an official record of 2,759 pounds of milk in 10 months. Toggenburg does, when mature, weigh from 100 to 135 pounds and mature bucks, from 150 to 175 pounds. Owing to the fact that Toggenburg goats are more plentiful here than other breeds, a good many grade goats of the Toggenburg type are found in various parts of the country. In fact, many herds have been established by crossing Toggenburg bucks on does of the American type.

Nubian milk goats, although considered a valuable breed, are not numerous in this country. They are natives of Nubia, upper Egypt, and Abyssinia. The colors of Nubians are black, dark brown, or tan, with or without white markings. They have a striking appearance, with drooping ears, a convex face, and a prominent forehead. Nubian bucks when mature weigh 165 pounds or more and mature does, 125 pounds or more. The Nubian breed is considered one of the best for milk production and the milk is noted for its high butter fat content; however, no figures are available on production for this breed.

There are also some Anglo-Nubian goats in this country. These are a very popular type of goat in England and are descended from crosses between the Nubian and goats of English origin. The predominant colors are black, tan, and red, with or without white. Some good specimens have shown a color approaching a roan, which is the color of the doe shown in figure 1, *C*. Anglo-Nubians are considered good milkers. Richards (*21*)[1] states that Nubians and Anglo-Nubians are less well adapted to cold climates than are the other breeds.

A scattering of Alpine goats are found in the United States and trace to an importation of 3 bucks and 18 does brought into California from France in 1922. The Alpines range in color from pure white to pure black with frequent white spotting on the neck, legs, or underneath the body. They are of large size and quite hardy, and they have excellent capacity for milk production.

The Maltese breed, while considered valuable in some parts of the world, is of no special importance in this country at present, except that it has had some influence on the type of goats in the Southwest. It is native to the island of Malta. The color is white and reddish brown or black. It is considered one of the best breeds for milk production.

In the southwestern part of the United States there is found a type of goat known as the Spanish Maltese, which is descended from crosses between the Maltese and goats of Spanish origin. It is said that at a former time many Maltese goats were taken into Spain and from there to Mexico and finally to Texas and New Mexico. This type of goat is white or grayish in color, but many have brown, bluish-black, or reddish spots. The ears are pendulous. It is asserted that some are very good milk producers.

The common, or American, goats (fig. 2, *A*) found in many sections of the United States, especially in the South, are of mixed origin. In many sections these goats have been bred for a great many years without the introduction of outside blood, so that in general conformation they are nearly uniform, being of medium size, somewhat short legged, and rather meaty in appearance. They do not show

[1] Italic numbers in parentheses refer to Bibliography, p. 1312.

Figure 2.—*A*, Common American doe no 66 used as one of the foundation does of the United States Department of Agriculture herd at Beltsville, Md. This doe produced 367 pounds of milk in a lactation period of 275 days. *B*, United States Department of Agriculture doe no. 214. This doe represents the third top cross of high-producing Saanen bucks on a foundation of common American does. This doe produced 1,796.3 pounds of milk in a lactation of 266 days.

the conformation of the Swiss breeds, and they are of various colors—brown of various shades, brown and white, black and white, bluish gray, and white predominate. Although a few goats of this type are occasionally found that are good milkers, the quantity of milk produced is usually small and the lactation period lasts only a few months. Yet by crossing common does with bucks of the Saanen, Toggenburg, and Nubian breeds for several generations, some of the very best milkers in the United States have been produced. Because of the scarcity of good milk goats, common does have been used largely for grading up with the improved breeds.

Distribution of Milk Goats in the United States and the World

With the exception of the dog, the goat is the most widely distributed of all domesticated animals, and the genus *Capra* is found throughout the world outside of the Arctic regions. Table 1 shows the distribution of goats of all types for those countries that reported an average of 500,000 or more during the 5-year period 1926–30. Although the types of goats are specified in only a few instances in census data, it seems probable that the majority of the goats reported are used for milking purposes. The total number of goats in the world is estimated at 189,000,000, of which 8,000,000 are classed as Angora goats.[1]

Table 1.—*Number of goats of all kinds in countries having an average of 500,000 or over for the period 1926–30*

Country	Average number, 1926–30	Country	Average number, 1926–30
	Thousands		*Thousands*
North America and Central America:		Africa—Continued.	
United States, total, goats	[1] 4,821	Tanganyika Territory	2,873
United States, Angora goats	[1] 3,785	French West Africa (total)	2,397
Mexico	[1] 5,984	Anglo-Egyptian Sudan	2,005
Dominican Republic	650	British Somaliland	1,800
South America:		Uganda	1,416
Argentina	[1] 5,647	Tunisia	1,370
Brazil	5,267	Belgian Congo	1,127
Venezuela	2,155	British Southwest Africa (total)	1,025
Chile	[1] 789	British Southwest Africa, Angora goats	32
Bolivia	713	Basutoland	956
Peru	638	Italian Somaliland	942
Europe:		Rhodesia (total)	883
Spain	4,524	Eritrea (Italian)	642
Greece	4,490	French Equatorial Africa	578
Germany	3,204	Ruanda and Urundi	510
Italy	[1] 1,892	Egypt	615
Yugoslavia	1,765	Asia:	
Portugal	1,579	Turkey, European and Asiatic, total goats	11,436
France	1,486	Turkey, European and Asiatic, Angora goats	2,925
Bulgaria	1,261	Iraq-Mesopotamia	1,757
Czechoslovakia	1,163	Persia (Iran)	8,000
Albania	790	Syria and Lebanon	1,566
Union of Soviet Socialist Republics	12,200	India:	
Africa:		British	38,336
Union of S. Africa, total goats	7,808	Native States	10,836
Union of S. Africa, Angora goats	1,588	Dutch East Indies	2,739
Nigeria and British Cameroons	5,181		
Kenya Colony	3,766		
Morocco	3,072		
Algeria	3,003		

[1] Figures from census of 1930.

[1] The proportion of Angora to milk goats in the United States is much different from that prevailing in most parts of the world. According to the 1930 census, milk goats constitute less than one-fourth of the total number of goats in the United States. In many countries, such as Spain and Germany, the proportion of milk goats to Angora goats is much larger.

The total number of milk goats [2] in the United States can only be estimated as no specific census figures are available. The total number of goats of all kinds in 1930 according to the census of that year was 4,821,000, of which 3,785,000 were specified as Angora goats. Only a small percentage of the 1,036,000 other goats, of short-haired type, could be classed as improved milk goats. In 1930 [3] the five leading States in number of short-haired [4] goats and kids were Texas with 185,737; New Mexico, 102,548; Arizona, 97,628; Georgia, 84,503; and Tennessee, 53,948.

Milk goats are found in practically all sections of the United States and in recent years have increased in numbers in the Eastern and Middle Western States. While California ranks eleventh in total number of short-haired goats, the milk goat industry in southern California has developed to a greater extent than in any other section of the United States. The dry, even climate, the abundance of feed, both wild and cultivated, and the favorable marketing conditions present opportunities not offered in most sections.

In a number of countries milk goats have been bred for many years, and in a few countries, Switzerland in particular, they have been brought to a state of considerable efficiency and perfection. In Spain goats are the chief source of the milk supply. In Europe and Asia the goat is used quite generally as a dairy animal, while in Africa meat and skins are the principal products.

PROPERTIES AND USES OF GOATS' MILK

Goats' milk differs in some respects from the milk of the cow. Chemical analyses of the two kinds of milk are shown in table 2.

TABLE 2.—*Composition of goats milk* [1] *and that of two common breeds of dairy cows*

Source of milk	Water	Total solids	Fat	Protein	Lactose	Ash
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Goat	88.02	11.98	3.50	3.13	4.55	0.80
Holstein-Friesian	87.50	12.50	3.55	3.42	4.86	.68
Jersey	85.31	14.69	5.18	3.86	4.94	.70

[1] Average of purebred and high-grade Saanen and Toggenburg does.

Considerable variability is observed in the composition of milk from different breeds of both goats and cows, between individuals in the same breed and even in samples taken from the same individual, especially when such samples are taken at widely different periods of lactation. The above results for the goat are based on analyses of milk from the herd kept by the United States Department of Agriculture at Beltsville, Md., while the results for the two breeds of dairy cattle are from data reported by the Associates of Rogers (*22*).[5]

[2] The term "milk goats" is one applied to goats that have been bred and developed especially for milk production. The term "Angora" is one given to that breed of long-haired goats which have been bred and developed especially for mohair production. The term "short-haired goats", as used herein, is one commonly applied to unimproved goats of mixed breeding that are sometimes used for milk production. In no case does the term refer to goats producing mohair.

[3] Fifteenth Census of the United States, Agriculture, v. 4. 1930.

[4] The term "short-haired goats" as used by the census probably includes some milk goats

[5] Italic numbers in parentheses refer to Bibliography, p. 1312.

Studies by Jordan and Smith (*11*) showed that there are no essential differences in the casein of goats' and cows' milk. Similarly, studies on milk from the Department of Agriculture herd show that there are no significant differences between these two kinds of milk in content of calcium, phosphorus, iron, and copper. Studies made in the nutrition laboratories of the Department on the vitamin content of goats' and cows' milk showed no marked superiority of one over the other. Jersey milk was found to contain somewhat more vitamin A, but goats' milk more of vitamins B and C. It was also determined that goats' milk has a much softer curd than the milk of either Holstein-Friesian or Jersey cattle.

Through the cooperation of the Department of Agriculture and Johns Hopkins University, normal infants were fed Holstein, Jersey, and goat milk. The milk used in these studies was boiled for 1 minute and was supplemented with orange juice and cod-liver oil. While the number of infants fed on any one kind of milk was too small to furnish conclusive results, no essential differences in health, general appearance, and well-being of the infants were observed, good results being obtained with each kind of milk.[6] The gains in weight were in proportion to the total nutritive contents of the milk. No attempts were made to compare the two kinds of milk on infants with a history of malnutrition. Goats' milk may be of value for infant feeding in cases of food idiosyncrasies, for many cases are on record in which children are able to utilize goats' milk, but not the milk of the cow.

The fat globules are much smaller in goats' milk and this characteristic, together with a softer curd, makes it easier to digest than cows' milk. Because of the small fat globules, which prevent the cream from rising to the surface, the ordinary method of obtaining cream by allowing it to rise is impracticable. By the use of the separator, however, practically all the butterfat can be obtained and it may be used satisfactorily for making butter. Several varieties of cheese are also made from goats' milk. To a limited extent, powdered, condensed, and evaporated goats'-milk products are being manufactured in the United States.

No figures are available concerning the total production or consumption of goats' milk and of the products made from it. In general, there has been only a specialized market for goats' milk and the development of goat dairy enterprises has been limited to a large extent by this market. The price of goats' milk has ranged from 10 to 50 cents a quart and sometimes even higher. There is one brand of evaporated, unsweetened goats' milk on the market which sells for 25 cents for a can of 6 ounces. This is equivalent to about 65 cents a quart for the original milk.

Studies on the Physiology of Milk Secretion

Cunningham and Addington (*8*) studied the effect of early breeding upon milk production. It was found that does freshening for the second time at 2 years of age produced significantly more milk than does that freshened for the first time as 2-year-olds. However, the does freshening for the first time at 2 years of age had somewhat

[6] Four infants were fed on goats' milk and 3 each on Holstein and Jersey milk. The results were in conformity with similar comparisons of the 3 kinds of milk on both kids and rats.

longer lactation periods. The greater production of the goats freshened first as yearlings is contradictory to the belief of many goat breeders.

The question of breeding does early or late in the lactation period has been studied by Brooks (*5*). He found that while delayed breeding tends to prolong the lactation period indefinitely, the later production is at a much lower level. Furthermore, breeding early in the lactation period did not seem to decrease the rate of production during the first part of lactation.

The goat is a seasonal breeder. Turner (*26*) investigatéd this question for goats of various breeds in the United States and found that estrous cycles in normal does occur quite regularly at intervals of about 21 days during the period from September to February. During the months from April through July, and perhaps mostly through August, estrous cycles are generally suppressed. Similar findings were reported by Kupfer (*13*) for goats in South Africa and in Switzerland.

By the injection of an extract prepared from the anterior lobe of the pituitary gland, Asdell (*2*) was able to bring about some improvement in milk secretion of goats in the late stages of lactation. No improvement was observed from injections made early in lactation, especially in the better milkers. Evans (*9*) was able to induce lactation in several virgin milk goats following the injection of a pituitary extract, and in one mature goat during her dry period. In cattle he reports that the Bureau of Dairy Industry of the U. S. Department of Agriculture has been able to get increases in milk yield following the injection of pituitary extract in some low-producing cows that apparently had a deficiency of this hormone. The yield returned to former levels as soon as the injections ceased. Good-producing cows did not respond. These results indicate that there is a relationship between the secretion of the pituitary body and the ability to lactate, but sufficient information is not yet available to make it possible to use this information in a practical way.

Turner and Reineke (*27*) observed that involution of the mammary gland (shrinking of the secretory tissue) was almost complete in a goat in the late stages of lactation, and that the stimulation of milking was ineffective in maintaining the secretory tissue in such goats. Their results suggest that attempts to increase the milk flow by the use of hormones will fail unless growth of the secretory tissue is first induced.

RESEARCH AND PRACTICE LOOKING TOWARD MILK GOAT IMPROVEMENT

In 1936 the Department of Agriculture undertook, as a part of the germ-plasm survey, to determine the status of milk goat breeding in the United States. Questionnaires were sent to experiment stations in those States where milk goats are raised in large numbers, and also to important private breeders whose names had been obtained from State experiment stations and from breed association secretaries. The following information was requested: (1) The name and registration number of important sires; (2) the number of each daughter and her dam; (3) the age when the doe was tested; (4) the number of days in milk; (5) the pounds of milk produced; and (6) the pounds of butterfat produced, and the percentage of butterfat, for each daughter and her dam.

The returns from private breeders were limited. While there are some herds of fairly large size, it appears that few breeders are keeping records on milk and butterfat production, although many breeders expressed a desire for such records and a willingness to cooperate in the keeping of records. Certainly no progress in locating superior germ plasm can be made until better records exist than those now available.

From this survey it was also determined that New Mexico is the only State now conducting research on milk goat breeding. This station has had an extensive breeding program under way since 1919 and the results are discussed in a later section.

Research in Milk Goat Breeding in the Department of Agriculture

Research was initiated with milk goats by the Bureau of Animal Industry in 1909 with the breeding of common or American does to bucks of the same type, with the purpose of developing a superior strain for milk production. Progress was slow and difficult and after 2 years of experimentation of this sort purebred bucks of both the Saanen and Toggenburg breeds were obtained for grading up the common does. The lines started from the top crosses of the original does by males of these two breeds were kept distinct. In each generation the best producing does were retained for top-crossing in the succeeding generation.

Progress has been slow since only a relatively small number of breeding does could be maintained and breeding activities were curtailed at various times. However, there has been some progress. The average length of the lactation period for the top-cross does, on the basis of the 1934 and 1935 results, has increased 145 percent and the average annual milk yield, 335 percent over that of the native does.[7] It should be pointed out that only six native does were available for comparison and the average length of lactation for these does was only 113 days.

The influence on both milk yield and length of lactation as a result of continuous top-crossing with purebred bucks is shown in table 3. With few exceptions, the does were approximately 24 months old at the beginning of lactation.

TABLE 3.—*Influence of top-crossing with purebred bucks on the milk yield and length of lactation of does during their first lactation*

Does (number)	Grade of does[1]	Milk yield: First 120 days (average)	Milk yield: Range during first 120 days	Lactation period: Total average length	Lactation period: Range in length	Increase in average milk yield over natives
		Pounds	*Pounds*	*Days*	*Days*	*Percent*
6	Native	[2] 325.2	253.2–445.2	113	107–122	----------
5	½	[2] 417.6	376.8–450.0	256	230–276	28.4
8	¾	466.7	295.5–554.6	273	205–333	43.5
13	⅞	470.4	313.3–698.2	235	137–309	44.6
18	15/16	496.0	306.2–707.0	256	144–366	52.5
13	31/32	491.4	156.7–807.8	244	122–302	51.1
7	Purebred	523.9	298.6–765.0	278	227–340	61.1

[1] Proportion of pure breedng. [2] Estimated milk yield for first 120 days.

[7] Total annual milk yield is dependent on increased production and persistency in lactation. Much of the increase in annual milk production of the top-crossed does was due to their greater persistency in lactation.

Since the length of lactation varied greatly, the quantity of milk produced by each doe during the first 120 days of her first lactation is used as a basis for the comparison of the productive abilities of does of the different top-cross generations.

As the trend in improvement of milk yield was similar for the top-cross does from the Saanen and Toggenburg bucks, the results for the two breeds were combined. A doe of the third top cross is shown in figure 2, *B*. The milk production of the does from the fourth and fifth top-cross generations was almost equal to that of the purebred does in the herd. No production data are available for grade does of more than thirty-one thirty-seconds pure breeding. A fourth top-cross doe produced 2,221 pounds of milk in 355 days, while the best purebred doe produced 2,297 pounds in 312 days. A number of the grade does had production records exceeding 1,600 pounds for one lactation.

The length of the lactation period also was increased as a result of the top-crossing, although a large part of the improvement was observed in the first top-cross generation. Since only six native does were tested, the average of 113 days observed for them may have been lower than the average for the population of does from which they were chosen.

A comparison of the milk production of does of different ages in the Department herd is shown in table 4. These results show that the period of maximum milk production for does is between 4 and 6 years of age. The length of lactation period also is greatest between the ages of 4 and 6 years but the change observed in length of lactation was not so great as that for milk production.

TABLE 4.—*Average milk yield of does of various ages in the Department of Agriculture herd at Beltsville, Md., 1930–35*

Age of does	Does	Average milk yield	Average length of lactation period	Age of does	Does	Average milk yield	Average length of lactation period
Years	*Number*	*Pounds*	*Days*	*Years*	*Number*	*Pounds*	*Days*
2	28	964.8	255	6	12	1,427.1	286
3	19	1,173.5	281	7	7	1,335.8	268
4	17	1,449.1	290	8	4	1,196.2	266
5	12	1,424.4	276				

A comparison of the purebred sires used in this herd, as measured by the sire index (calculated by the commercial form of the Mount Hope index, as described by Prentice (*20*)), showed that marked differences exist in the ability of sires to transmit their characteristics to their offspring. None of the sires possessed the necessary inheritance for raising both the milk yield and the length of the lactation period of all his daughters.[8] However, more sires increased the milk yield of their daughters than increased the length of the period of lactation.

[8] This study would indicate that all the sires compared are heterozygous for some of the genes affecting milk yield and length of the lactation period.

Research at the New Mexico Agricultural Experiment Station

Since 1919 the New Mexico Agricultural Experiment Station has conducted experiments to determine the improvement that might be expected from grading up native does of the Southwest with purebred Toggenburg bucks. The native does were descendants of the goats brought into the United States by the Spaniards. Since its initiation, the experiment has been expanded to include such studies as the inheritance of horns and wattles, length of gestation, prolificacy, the sex ratio, and a determination of the effects of inbreeding and outcrossing on milk production, and the birth weight of kids.

The foundation animals for the breeding experiment consisted of 10 native yearling does that came from a herd in which there was no apparent evidence of improvement by the use of improved bucks of either Angora or milk type. Milk records were secured on 8 of the 10 foundation native does and their progeny.

The improvement in production resulting from top crosses of purebred Toggenburg bucks on native does and their resulting offspring is shown in table 5 in comparison with the production of purebred does. Each of the does was approximately 2 years old at the beginning of her lactation period. In all cases the quantity of milk produced by a doe was corrected to a butterfat basis of 4 percent by use of the formula of Gaines and Davidson (*19*).[9]

Table 5.—*The effect on milk production of using purebred Toggenburg bucks on native does and their offspring*

Breeding	Animals	Milk	Butterfat		Fat-corrected milk	Length of lactation period	Gain over native does [1]	Dam-daughter pairs	Daughters higher than dams in f. c. m.[2]	
	Number	*Pounds*	*Percent*	*Pounds*	*Pounds*	*Days*	*Percent*	*Number*	*Number*	*Percent*
Native does	8	522.2	5.0	26.14	611.0	230	0	-------	-----	-----
½ Toggenburg	22	1,059.7	3.99	42.23	1,057.6	279	73	22	21	95
¾ Toggenburg	30	1,133.0	3.62	41.14	1,070.3	282	75	28	9	32
⅞ Toggenburg	27	1,319.4	3.61	47.60	1,241.7	288	103	26	21	81
15/16 Toggenburg	19	1,505.2	3.73	56.16	1,444.7	303	136	18	9	50
Above 15/16 Toggenburg	10	1,311.4	3.82	50.03	1,274.7	300	109	9	2	20
Purebred Toggenburg	22	1,488.7	3.76	55.96	1,436.7	293	135	16	10	63

[1] Gain is based on increase in production of fat-corrected milk. [2] Fat-corrected milk.

Marked increases in milk production were obtained from the top-cross does, the greatest increase occurring in the first generation. From the fourth top cross, does equaling the production of the purebred females were obtained.

A number of does in the station herd have made creditable records under the rules for advanced registry of the American Milk Goat Record Association, several being leaders in their respective classes. One of these, Val Verde's Zula 25467, has a record of 2,759.0 pounds of milk and 100.2 pounds of fat. Another, NMAC Mary Ann, a daughter of Val Verde's Zula, has a record of 2,570.4 pounds of milk

[9] This formula is as follows: f. c. m. (fat-corrected milk) = 0.4 m + 15 f. M represents weight of milk and f weight of fat. This formula expresses the energy produced by an animal in the form of milk and butterfat as an equivalent amount of 4-percent milk.

and 77.08 pounds of fat, while several others have records exceeding 2,500 pounds of milk and 90 pounds of fat. Two of these high-producing does, Laura Lorenzo 35768 and NMAC Amelita 35769, are twins.

During the course of the experiment at the New Mexico Station, line-breeding has been practiced to three outstanding bucks in an attempt to fix the desirable characteristics of the family from which these bucks came. The production of the inbred and outbred daughters from these males is shown in table 6.

Table 6.—*A comparison of inbred and outbred daughters from three outstanding sires in the New Mexico herd*

Name and no. of sire	Average production of—								
	Inbred daughters					Dams of inbreds			
	Inbreeding [1]	Tested	Milk	Butterfat		Milk	Butterfat		
	Pct.	*Number*	*Lbs.*	*Lbs.*	*Pct.*	*Lbs.*	*Lbs.*	*Pct.*
Leonidas 3820 (A. M. G. R. A.)[2]	25.0	7	1,080.3	39.27	3.63	1,093.4	47.43	4.33
	37.5	1	1,108.2	34.30	3.09	949.8	28.97	3.05
Rosemont's Angelus 13201 (A. M. G. R. A.)[2]	25.0	10	1,101.4	46.12	4.18	1,176.4	42.43	3.61
Val Verde's Lorenzo 30551 (A. M. G. R. A.)[2]	25.0	22	1,306.9	50.99	3.90	1,523.6	58.23	3.82
	37.5	6	1,218.0	49.20	4.04	1,278.5	47.26	3.69

Name and no. of sire	Average production of—						
	Outbred daughters				Dams of outbreds		
	Tested	Milk	Butterfat		Milk	Butterfat	
	Number	*Lbs.*	*Lbs.*	*Pct.*	*Lbs.*	*Lbs.*	*Pct.*
Leonidas 3820 (A. M. G. R. A.)[2]	19	1,094.2	44.05	4.02	548.9	27.67	5.04
Rosemont's Angelus 13201 (A. M. G. R. A.)[2]	35	1,201.6	43.02	3.58	1,078.3	42.05	3.89
Val Verde's Lorenzo 30551 (A. M. G. R. A.)[2]	29	1,624.6	60.45	3.72	1,126.4	41.21	3.65

[1] Calculated by method of Wright (*33*). [2] American Milk Goat Record Association.

The effect of the inbreeding in general has been to lower slightly the milk production of the inbred does in comparison with the production of their dams, whereas the outcrossed daughters have exceeded their dams in milk production. In the production of butterfat, however, as measured by the percentage of butterfat in the milk, the inbred does did somewhat better than the outbred does. While it would appear from these results that close inbreeding is not a good practice for the average breeder of goats, it is to be hoped that experiment stations conducting breeding experiments with milk goats, and likewise some of the larger breeders, can practice some inbreeding in their herds.

Much experimental work on animals and plants has shown that inbreeding is a certain method for increasing the purity or homozygosity of inherited characteristics. If accompanied by rigid selection, good inbred strains may eventually be isolated. Individuals of these strains, because of their greater purity for certain desirable charac-

teristics, should have a greater chance to transmit these characteristics when outcrossed to unrelated goats, and they may be valuable parental material in other ways. It should be emphasized, however, that the use of close inbreeding for animal improvement is still in the experimental stages, and that it is not recommended for the average private breeder.

In addition to the studies on production, the New Mexico station has presented data on the length of the gestation period, on fertility and fecundity, and on the sex ratio.

A total of 144 gestation periods were recorded, 115 being for does over 18 months old and 29 for does under 18 months. The mean

Figure 3.—United States Department of Agriculture Saanen doe no. 412 with her quadruplet kids. Quadruplets are uncommon in milk goats, only 3 sets being recorded in a total of 617 parturitions in the Department herd. In the herd of the New Mexico Agricultural Experiment Station 4 sets of quadruplets have been recorded in a total of 144 parturitions. Instances of a larger number of kids at one parturition are very rare.

length of the gestation period for all does was 149.9 days, with a range from 136 to 157 days. For the younger does the range was from 136 to 154 days and for the older does from 139 to 157 days. The mean for both groups was 149.9 days.

Fertility in this herd was high. From 152 matings a total of 144 conceptions was secured; 127 of these were from single services, 13 from the second, 3 from the third, and 1 from the fourth service. From the 144 parturitions 286 kids were produced, the distribution of single and multiple births being as follows: Single, 40; twins, 70; triplets, 30; and quadruplets, 4. A somewhat higher proportion of multiple births was observed for the older does. A Saanen doe with quadruplet kids is shown in figure 3.

A preponderance of males was observed, the ratio of males to females being 115 to 100, for a total of 363 kids examined. This is a somewhat lower proportion of males than has been reported by other investigators.

Private Organizations Sponsoring Improvement

Promotion of the interests of milk-goat breeders in the United States has depended largely on various breed associations and on State and local organizations of breeders. Through the medium of exhibits at State and county fairs, and by advertising in various periodicals mostly devoted to the promotion of goats, much interest in milk goats has been created in many sections of the country.

At the present time three associations are registering goats—the American Milk Goat Record Association of Vincennes, Ind., the International Dairy Goat Record Association, at Lincoln, Nebr., and the American Goat Society, Inc., of Wayland, N. Y. Of these, the first mentioned is the oldest and largest. It was organized in 1903, and by the end of October 1936 had recorded 51,118 purebred and grade goats. The second association was organized in 1927 and had recorded a total of 2,323 purebred goats, while the third organization was established in 1935 and had registered 1,527 purebred animals by the end of October 1936.

The American Milk Goat Record Association has established an advanced registry and is sponsoring the testing of does for milk and butterfat production. Its requirements for advanced registration are comparable in some respects with those adopted by the various organizations promoting advanced registry of dairy cattle.[10] A total of 201 females have met the requirements for advanced registry—123 Toggenburg, 60 Saanen, 11 Nubian, and 7 native does. In 1936 the American Goat Society, Inc., established a herd-improvement registry for the purpose of obtaining individual production on each doe in the herds registered under this plan.

In addition to the registry associations there are many State and local societies that are promoting the milk-goat industry in various ways. Three papers—the Goat World, the Dairy Goat Journal, and the American Goat Herd—are devoted primarily to sponsoring the interests of milk-goat breeders.

Needs of the Future

Much progress has been made by some breeders of milk goats in improving their herds. While figures are not available on the aver-

[10] The advanced registry of the American Milk Goat Record Association has been divided into two divisions, one designated as class A and the other as class B. The division known as class A is divided into classes A, B, C, D, E, F, and G, depending on the age of the animal at the beginning of the test. In order to enter a doe in the 10-month, or class A division, it is necessary for the owner to weigh the milk from each individual milking and keep a proper record of the weights throughout the testing period. A copy of this record must be forwarded to the association at the end of each month. The doe must also be tested for a 24-hour period each month by a representative from the State agricultural college or experiment station, in order to determine the amount of fat in the milk. The testing period cannot exceed 10 months but may be for any period under this that the owner may desire, the tests commencing on the seventh day after parturition. However, a 2-year-old doe must produce at least 52 5 pounds of fat or 1,500 pounds of milk during the consecutive test period in order to be admitted to advanced registry. For each day that the doe exceeds 2 years at the beginning of the test, and up to 5 years, the required production is increased by 0.007 pound of fat or 0.2 pound of milk per day. No further increase is required for does older than 5 years. The class B, or short-time division, of the advanced registry requires that a doe produce an average of 10 pounds of milk during three 24-hour test periods, taken at least 30 days apart. This record to be supervised by three disinterested persons who make sworn statements in regard to the production. Bucks are entered in the advanced register when they have sired three advanced-registry daughters out of three different dams.

age production of milk goats in this country, certainly it is far below that of the better herds and probably below the average production of herds in such countries as Switzerland, where the goat plays a greater part in domestic economy than in the United States.

There can be no doubt of the need for improvement in the milk production of goats in the United States. While it is not to be expected that the goat will supplant the dairy cow to any great extent, there are sections of the country where good milk goats would contribute materially to the welfare of many families. The facts that a goat can be kept where it would be impossible to keep a cow and at the same time will supply sufficient milk for the average family, are features that seem to make goats suitable for families of low incomes living on small acreages in suburban districts, in mining districts, and in other areas where a good supply of milk is not available and the keeping of cows is impracticable.

In addition to milk production, attention should be given to improvement in the fat content of the milk, to increasing the average duration of lactation, to the improvement of fertility and the development of strains that will breed at any season.[11] Practically no attention has been given to these characteristics, all of which are important.

But improvement of the goat alone will not solve the problems of the industry as a commercial business. If an industry is to grow, it must have new or better markets for its products. Research is greatly needed to develop uses for goat products, and one of the chief activities of breed organizations should be to encourage research in this field. Among the problems that might well be studied are (1) the value of goats' milk for the feeding of infants, invalids, and persons allergic to cows' milk and its products, (2) its value for the making of cheese of various types, (3) methods for the preparation of condensed milk in order to make it more widely available, (4) the creation of a greater demand for goat meat, by advertising and the development of new and better recipes for its preparation, and (5) studies on the economics of production under various systems of farming.

The Part of the Breeder in Future Milk Goat Improvement

Future improvement in milk goats must come largely through the efforts of breeders. Fundamental research is needed to guide breeding efforts, but research of this kind will be undertaken only at the demand, and with the support and encouragement, of breeders. In addition, breeders can do much themselves to improve the goat. Practices that should be of general benefit would include:

1. The keeping of more complete records on milk and butterfat production, fertility, and fecundity of the goats in the breeding herd. Such records are vital to breed improvement, and the germ plasm survey conducted by the Department of Agriculture indicates that many prominent breeders have been lax in keeping such records.

2. The development of a more extensive record-of-performance program that will enroll the better breeders. Fortunately the foun-

[11] Most goats breed only during certain months of the year, generally from September to March. This fact provides a problem for the producer who has need for a continuous milk supply. A few investigators have given attention to the problem. It has been suggested that perhaps the most economical solution is the breeding of does that come in heat regularly throughout the year. To what extent such does occur is not known but it seems probable that such strains might be developed by the application of a proper breeding program.

dation for such a program has been laid and it should be encouraged to the fullest extent. Dairy breeders have made much progress in the use of record-of-performance tests and goat breeders can utilize many of these findings in the development of their own program.

3. The more extensive use of proved sires. It is well known that sires differ greatly in their ability to transmit inherited characteristics to their offspring. While the record of his ancestors furnishes some information about the value of a sire, the surest way of determining this is to study the records of his daughters. Once a sire has proved his ability to transmit desirable characteristics, provision should be made to use him to the fullest extent. Because of the wide distribution of goat breeders and the relatively small size of the herds, this will prove difficult in many cases. However, the need for the use of such sires is so great, if proper progress is to be made, that breeders and breed associations should make every effort to develop means whereby exchanges of such sires could be made between breeders.

4. The development of a better spirit of cooperation among breeders. Too frequently in the past there has been a tendency for the development of factions. This has resulted in tendencies for various groups in the industry to be working at cross-purposes. For instance, several breed associations have been established, each recording all breeds of milk goats. The result has been to lower the effectiveness of the breed associations in sponsoring breed promotion and improvement. It also makes it more difficult for the breeder to record his animals, especially if transfers from one association to the other are desired. With the relatively small number of purebred milk goats in the United States, one vigorous organization receiving the support of the whole industry certainly would seem to be sufficient.

5. Finally, more consideration needs to be given to the development of better procedures to guide breeders in the selection of breeding animals. Much information on the basic problems of animal breeding that should be of great use to goat breeders is contained in the 1936 Yearbook of Agriculture.[12]

The improvement of the milk goat, in common with the improvement of other species of livestock, is a large task that will require the best efforts of the breeder, the research worker, and all other interested agencies.

GENETIC STUDIES OF THE GOAT[13]

SINCE the improvement of goats has rested largely in the hands of private breeders and very few research agencies have had projects pertaining to goat husbandry in any form, genetic studies of this species have lagged. Nevertheless, some facts concerning the genetics of various characters have been reported, although most of the conclusions must be considered as tentative.

The inheritance of horns in goats has been studied by Lush (*14*) Warwick (*29*), Addington and Cunningham (*1*), Asdell and Crew (*3*), and Asdell and Smith (*4*). The evidence in each case strongly suggests that the polled and horned conditions constitute a pair of Mendelian characters, the horned condition being recessive and due

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[12] See particularly pp. 119–206, 831–862, 907–923, and 997–1069.

[13] This section is written primarily for students and others professionally interested in genetics or breeding.

to a single recessive gene. In a few cases, however, individuals with scurs (imperfectly developed horns, usually without an attachment to the bone) were observed, but the data were too few to warrant an attempt to interpret the significance of the scurs. Muller (*18*) investigated the inheritance of the multihorned condition in goats but found that, while the character is inherited, the mode of inheritance was complex.

The mode of inheritance of wattles—sometimes called tassels—has been investigated by Asdell and Smith (*4*), Lush (*14*), and Addington and Cunningham (*1*). The evidence indicates that the wattled condition is dominant over the nonwattled condition and that one pair of genes is concerned. The exact manner of inheritance of the bearded condition has not been determined, but Asdell and Smith suggest that it is a sex-limited character dominant in the male and recessive in the female.

An inherited nervous instability of the goat has been reported by White and Plaskett (*32*), Hooper (*10*), and Lush (*15*). If suddenly frightened or surprised, goats with this affliction become rigid and the worst frightened usually fall. The spell usually lasts from 10 to 20 seconds. The animals recover the use of the muscles in the fore part of the body first, and on recovery often start moving away with the rear quarters dragging or very stiff. After being frightened once, the goats cannot be affected again, regardless of the extent of fright, until 20 to 30 minutes have elapsed. These goats apparently were quite unable to jump over obstacles of ordinary height. The mode of inheritance has not been determined.

The presence of short ears in the goat has been reported by Wassin (*31*) and Käb (*12*). Wassin suggests that one pair of genes is involved and that long ears are incompletely dominant. This would account for the three types of ears observed, the homozygous (*AA*) being long, the heterozygous (*Aa*) intermediate, and the recessive (*aa*) type being short. The short ears described by Käb, on the other hand, were dominant. In neither case, however, was the mode of inheritance definitely determined.

Much variability in color and marking occurs in the goat. The chief colors observed are white, brown, tan, red, roan, gray, black, fawn, and cream, but several other colors occur less frequently. Relatively little is known concerning the mode of inheritance of the various colors and the interactions of the genes concerned.[14]

Cryptorchidism (the condition in which one or both testes fail to descend into the scrotum) occurs quite commonly in the goat, and Warwick (*30*) and Lush, Jones, and Dameron (*16*) have shown that the condition is inherited, though the exact mode of inheritance has not been determined. At least two pairs of genes appear to be involved. Abnormalities of the reproductive system, which take the form of an intimate mixture of male and female parts belonging to the accessory

[14] Lush (*14*) considers that solid white, as found in the Saanen, is epistatic to all colors, this being in agreement with the opinion of Asdell and Smith (*4*). The latter, however, suggests that there is another type of white, a light cream, which may be due to an extreme type of spotting. Lush suggests that there is a tendency for black to be epistatic over nonblack and for extensive white spotting to be epistatic over nonspotting. Asdell and Smith, on the contrary, suggest that black may be the lowest term in an allelomorphic series of black, chocolate, fawn, and cream, the last color being dominant to all others. They suggest that brown is epistatic to all colors of the black series and, also, of the red and tan series, with the red and tan being hypostatic to the black series. Gray and roan appeared to be epistatic to the red and tan, and to the black series but hypostatic to brown.

sexual organs, are rather common in the goat, according to Crew (*7*). Since the abnormalities occur more frequently in some districts than in others, and because certain individuals in successive matings produce one of more of these intersexual offspring, it would seem that the condition is inherited. Nothing has been reported on the mode of inheritance.

Calder (*6*) has studied the incidence of multiple births in the goat and believes that prolificacy is a character controlled to some extent by genetic factors. The male appears to be equally influential with the female in transmitting the potentialities for multiple births. Calder suggests that most effective results will be obtained in selecting for prolificacy if due consideration is given to the prolificacy of both strains, and to the actual size of the litters from which the females and males are chosen.

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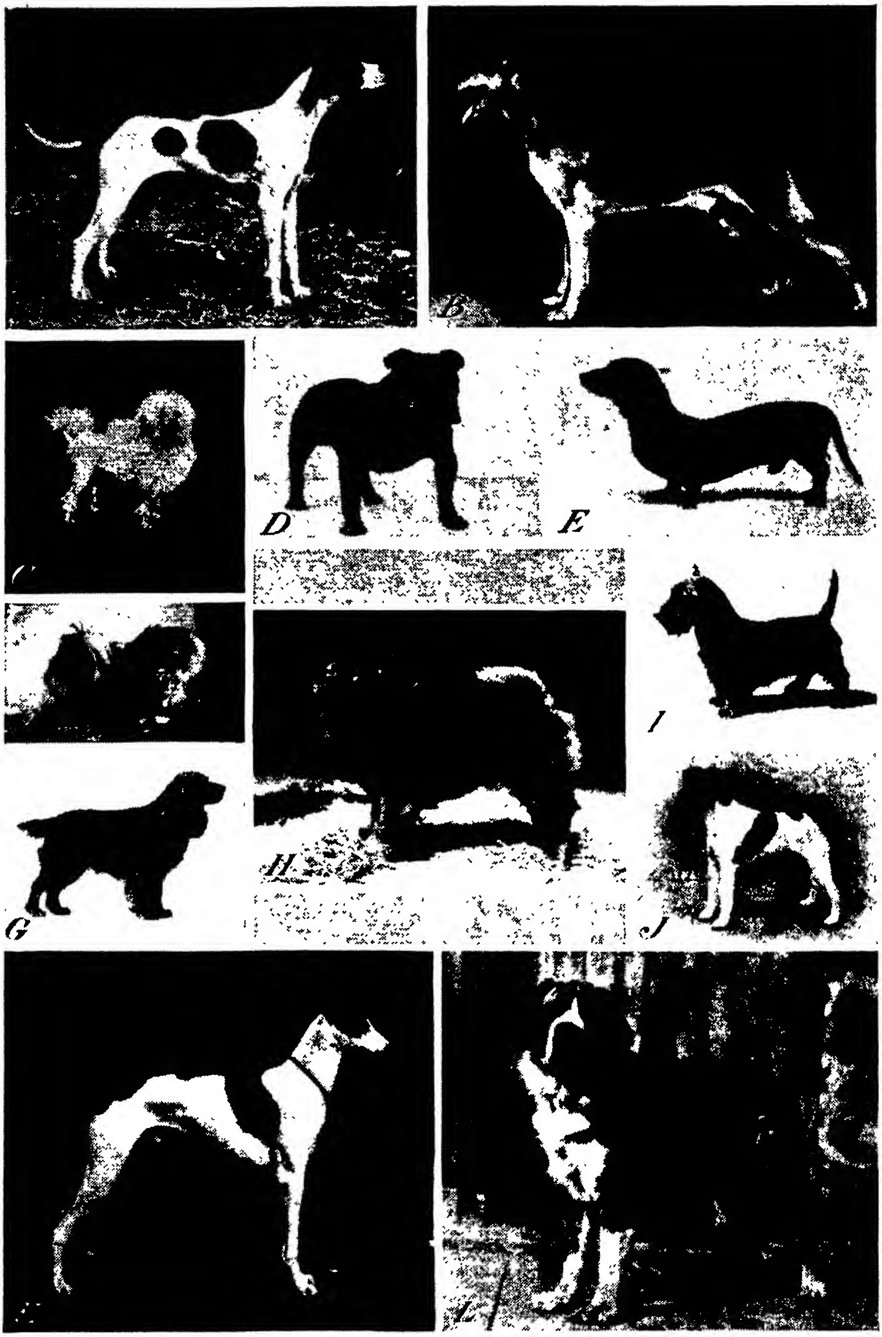

Figure 1.

(Legend on opposite page.)

HEREDITY IN THE DOG

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NO OTHER animal serves so many widely different purposes or has been so plastic in man's hands as the dog. Those characteristics by which dogs differ most from other domestic animals and which make them especially useful to man are largely of a psychological nature such as intelligence and willingness to cooperate. This can be especially appreciated by one who has watched a trained sheep dog working a quarter or half mile away from his master, yet obeying every signal that his master gives.

Partly because of their original inheritance and adaptability and partly because of the great variability that has resulted from centuries of selection, dogs today serve man as hunters, retrievers, guards, companions, aides in war, herders of livestock, police aides, guides, draft animals, entertainers in sports and shows, subjects in medical and scientific investigations, scavengers, fur bearers, and in case of necessity as food. Many of these uses can be subdivided and doubtless others might be given.

The range in size is so great that some animals in the largest breeds weigh 100 times as much as other normal individuals of the smallest breeds. An Irish Wolfhound standing on his hind legs can often look over the head of a tall man, while some full-grown Chihuahuas may stand comfortably on one's outstretched palm. Not only in size but in form, physique, temperament, aptitude, and intelligence there is great variation. Long, short, wide, narrow, tall, squat, slender, chunky, graceful, awkward, excitable, placid, robust, delicate, intelligent, stupid, friendly, savage, affectionate, self-contained, dignified, ridiculous, ugly, and beautiful are terms that might be aptly applied to different breeds and individuals. Figure 1 illustrates some of the wide variations in type.

In many of the breeds there is a so-called "standard" size, but there also may be a small or "toy" size, and sometimes a giant size. There are varieties with smooth, wire-haired, curly, long, stand-off, or corded coats.[1] Some breed standards permit all colors, others certain vari-

[1] A stand-off coat is a long profuse coat with the hair standing straight out from the body as in the Pomeranian and Chow. A corded coat is a coat of long curly hair matted together in the form of long ropelike cords as in the corded poodle.

Figure 1.—Variation in body form, type of coat, and color patterns as shown by some popular breeds of dogs in the United States. *A*, Pointer; *B*, German Shepherd; *C*, Toy Poodle; *D*, Bulldog; *E*, Dachshund; *F*, Pekingese; *G*, Cocker Spaniel; *H*, Chow; *I*, Scottish Terrier; *J*, Fox Terrier; *K*, Greyhound; *L*, St. Bernard. (*C*, *D*, and *L* by courtesy of G. Howard Watt, Inc.)

ations in color, and others only a single color or color pattern. Later in this article the causes for much of this variation will be discussed.

ORIGIN AND DOMESTICATION OF THE DOG

It is certain that doglike animals existed on the earth thousands of years ago. The origin of the dog (*Canis familiaris*), however, is not known. There is considerable speculation as to whether dogs originated from such present-day wild species as wolves, jackals, and dingoes, with which they will interbreed (fig. 2), or from other forms now extinct

Quite probably they trace to more than one of these sources. It has often been supposed that the fox, which has many doglike characteristics, was one of the ancestors of the dog. However, few, if any, authentic cases of successful crosses between these two species are known,[2] although numerous unsuccessful attempts to cross them have been reported. Accordingly, it appears improbable that the fox has played a very large part in the ancestry of our present dogs.

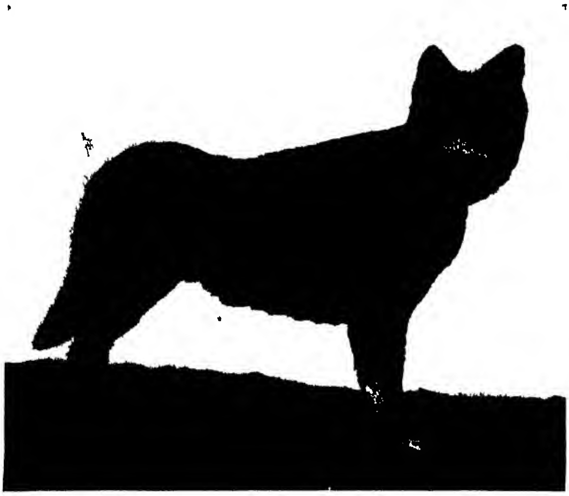

Figure 2.—Hybrid from a German Shepherd dog and a female wolf. (Photograph by courtesy of John Gans and Fachschaft für Deutsche Schaferhunde after von Stephanitz (54))

Students of the antiquity of the dog, Studer (*57*, *58*),[3] Breuil (*7*), Elliot (*15*), Osborn (*46*), Allen (*2*), von Stephanitz (*54*), and Clark (*10*) are agreed that dogs were domesticated before any of the other animals, but how long ago they do not know. In Europe bones of dogs have been found associated with the remains of men who invaded Europe at the close of the Paleolithic or Old Stone Age, and at the beginning of the Neolithic or New Stone Age. Since earlier remains of dogs have not been found in Europe, apparently they were brought to that continent by the pre-Neolithic peoples and were probably already partially domesticated, serving possibly as scavengers and guards and for food. This makes it seem probable that the dog was first domesticated in Asia at an even earlier date. Somewhat more recent evidence of domestication has been left us in the form of crude pictures carved by prehistoric man (fig. 3) showing dogs used in the chase (*8*, *35*).

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[2] Schmid (*53*) reports a successful cross between a fox and dog by Heck, in Germany

[3] Italic numbers in parentheses refer to literature cited, p. 1328.

Dogs as Farm Animals

Dogs have held an important place in agriculture and rural life for centuries. Probably they have been most important to the American farmer in guarding property, herding livestock, contributing to the sport and the larder of the master when he goes hunting, helping exterminate vermin, and as companions and pets. While it is impossible to estimate the value of these services, one can hardly imagine a cheaper or more efficient guard service for the farm than that furnished by a good watchdog, and if the same animal serves in other ways, as it often does, one can be sure that its value considerably exceeds the cost of keeping it. The value of dogs as companions, especially where people lead rather isolated lives, as they sometimes do in certain agricultural districts, is often underestimated. And what other animal gives the growing boy, either on the farm or in the city—or the growing girl, for that matter—as good an opportunity

Figure 3.—Prehistoric rock tracing representing reindeer, a horse in a boat, men, and dogs. Cut in the quartz at Massleberg, Skee Parish, Bohuslän. Height, 5 feet; width 12½ feet. (Courtesy of Cassell & Co., London, after Leighton (35).)

JUST *as some outstanding advances in other scientific fields—advances of very great value to humanity—have been made with the help of dogs, so their use in certain fields of genetic research seems to offer the most practical means of attacking some very important but difficult problems, notably those connected with the inheritance of psychological characteristics. Because they show so wide a range of intelligence, aptitudes, and temperament, and can be handled easily dogs appear to be better adapted to studies of this kind, especially with our present limited methods of measurement, than any other animal. Aside from the possibility of improving one of our most useful animals through such studies, there is the still more significant possibility of adding materially to knowledge of mammalian genetics, especially the inheritance of psychological traits—a field in which relatively little progress has been made.*

to learn self-control and consideration through the care and control of his pet?

According to an old saying, there is no good flock without a good shepherd and no good shepherd without a good dog. There are without doubt some exceptions to this, but there is no doubt that a trained herding dog is a great help and under some conditions indispensable in handling livestock. Many farmers enjoy hunting so that good hunting dogs are found on many farms. If one were to estimate the percentage of the 6,812,350 farms [4] in the United States that have at least one dog from the sample of which he has personal knowledge, it would certainly be very high

PRESENT STATUS OF GENETIC RESEARCH ON THE DOG

Although dogs have been domesticated for many centuries and have been successfully molded into many forms adapted to man's uses by the processes of heredity and selection, most of the breeds we know today have originated in comparatively recent time, and up to within a few years ago there had been very little, if any, breeding work with dogs that could be considered of a scientific nature.

However, there is a considerable store of scientific information concerning various aspects of the dog. Anatomists, physiologists, and psychologists have found the dog an excellent subject, especially in connection with medical research, for studying mammalian characteristics. In fact the diet, physiology, and temperament of dogs make them indispensable for certain types of experiment. Some of the outstanding advances in physiology, psychology, and medicine have been made with the help of dogs, as for example the work on conditioned reflexes by Pavlov (*48*) and much of the fundamental information on artificial respiration, and the control of diabetes and pernicious anemia (*9*)

In addition to the gain for humanity that has resulted from these experiments, dogs have been used, of course, in the study of their own disorders. The control of hookworm following the work of Hall (*19*) and of distemper resulting from the investigations of Dunkin and Laidlaw (*13*, *14*, *30*, *31*, *32*, *33*), who were provided with funds by the Field Distemper Council in Great Britain, has been made possible by the use of a relatively small number of dogs in the laboratory.

Although the results obtained in some of these researches indicate that the dog would serve as an excellent subject in the study of certain aspects of mammalian genetics, few systematic attempts have been made to obtain information on inheritance in this animal. However, many reports dealing with various aspects of the genetics of the dog have been published. The characters reported in these papers will be considered in this article in the following order: (1) Cytological (concerned with the chromosomes in the cell), (2) psychological, (3) morphological (concerned with form and structure), and (4) color.

Investigators are in disagreement as to the number of chromosomes in the dog. Thus Malone (*40*) has reported the number in the body cells as being 21 and 22 in the male and female, respectively; Minouchi, according to Oguma and Kakino (*44*), has reported 78 chromosomes in the body cells of both the male and the female; Painter (*47*)

[4] 1935 census figures.

has reported the number to be about 50, probably 52; while other investigators have found intermediate numbers (*29*).

Mental Characteristics and Temperament

In the study of mental characters psychologists have been able to measure various abilities of dogs such as the speed with which they form conditioned reflexes or immediate reactions to a given situation constantly repeated; their powers of discrimination with regard to visual objects and sounds of different kinds; their ability to make delayed responses to stimuli; and their ability to solve problems such as the opening of a box to get food or finding their way out of a maze or labyrinth. Since most such measurements are difficult to make accurately and require considerable time and expense, practically no information exists on the variation in these abilities among dogs of the various breeds and strains or on the mode of their inheritance.

Some information has been collected regarding the inheritance of certain aptitudes in dogs, as is shown in the appendix. For example, both Marchlewski (*41*) and Whitney (*64*) have reported that the aptitude for hunting with the head carried high appears to be dominant to the aptitude for hunting with the head carried low when certain strains or breeds of dogs are crossed. Although the list given seems impressive, it presents information on relatively few of the great variety of aptitudes possessed by dogs and most of the conclusions are based on a few observations only and have not been completely confirmed.

One of the best studies of temperament in dogs and the practical application of genetic principles to breeding dogs with superior abilities is that of Humphrey and his associates in producing and training dogs for leading the blind, and for police and army service, at Fortunate Fields, Switzerland (reported by Humphrey and Warner (*22*)). The tests used were largely subjective judgments by the trainers and while it was apparently impossible for them to determine the exact mode of inheritance of most of the characters, they were able by assuming that certain of these characters were largely controlled by a few major genes to make marked progress in producing superior animals.

Body Characteristics

In addition to mental traits, such body characters of the dog as conformation, functioning of internal organs, fertility, and resistance to disease play an important part in his usefulness. The body characteristics that have been studied genetically are listed in the appendix. Of particular interest in this connection is the work being carried on in this country by Stockard (*55*) and his associates at the Cornell University Medical College on the genetics of modified endocrine secretion and of associated form patterns—such as head shape—among dog breeds. (See the reported findings of Stockard and Vicari in the appendix.)

Although the color of the animal is a body character, it is so easily differentiated from other characters that it seems best to consider it separately. The third part of the list (p. 1337) gives the color characters in dogs for which information concerning the mode of inheritance has been reported.

On the whole, where more than one investigator has reported on the inheritance of a color factor, the results have been similar or the differences can be reasonably well accounted for. There appear to be marked similarities between color inheritance in dogs and that in rodents and in other carnivora (*18*), which makes some of the conclusions appear reasonable even where the evidence from dogs themselves is rather scant. No cases of proved linkage have been reported. There is, however, fairly good evidence that there are a number of allelomorphic (alternative) series of genes that affect color in the dog. These have been summarized briefly in table 2 in accordance with what seems to be the best evidence available. Some genes exhibit multiple effects, such as those caused by the gene for dominant irregular spotting, which in addition to affecting the coat color produces defective sight and hearing, frequently a reduction in general vigor, and sterility in the female (pp. 1333, 1936, and 1339).

Probably the greatest contribution of the science of genetics to practical breeding has been the formulation of a definite system of inheritance. This system furnishes the basis for a rational approach to breeding problems. However, at present it is difficult, for several reasons, to make specific recommendations on many practical problems confronting the dog breeder—the breeder's aims are extremely diversified; the dogs themselves exhibit such tremendous variations; there are not nearly enough known facts on inheritance in dogs to solve most of the problems of practical importance; and many practical men have not yet familiarized themselves with general genetic principles. (The discussion of these principles in introductory articles in this Yearbook will probably be found helpful in this connection.) This emphasizes the need for encouraging research on inheritance in dogs and for organizing breeders so that they can obtain information with regard to specific problems and can at the same time contribute to the knowledge of inheritance in dogs from their own records.

One method of encouraging improvement in the animals themselves would be to offer prizes at dog shows on the basis of the breeding record of an animal instead of almost wholly on the basis of its individual appearance or performance. Genetics has very definitely shown that in many instances the appearance of an animal is not a reliable basis for judging its value as a breeder. Its real breeding value depends on its ability to pass on desirable characters and combinations of desirable characters to its descendants. Because of the effect of dominant genes, the appearance of an animal may give no hint of the presence of recessive genes for quite opposite characters, more or less covered up by the dominants. Thus a short-legged dog may carry the gene for normal legs, which would show up in some of his descendants if they received the same recessive gene from the other parent. Similarly, a black dog may carry the gene for liver color. (See pp. 1334 and 1337.)

Not only individual genes but the particular combination of genes that an animal inherits also determines its appearance or performance. Since most animals are very mixed in their inheritance, they are capable of transmitting a large number of different combinations of genes to their offspring. For example, a dog of intense agouti or wild gray color without white spots may carry the genes for dilute coat color, for nonagouti, and for piebald white spotting. When this dog

was mated with an animal of similar mixed genetic composition, one would expect, if agouti, intense coat color, and absence of piebald white spotting are considered to be completely dominant,[5] to get puppies of eight different types so far as appearance is concerned, provided enough puppies are produced: (1) Intense agouti without white spots, (2) intense agouti with white spots, (3) intense nonagouti without white spots, (4) dilute agouti without white spots, (5) dilute agouti with white spots, (6) intense nonagouti with white spots, (7) dilute nonagouti without white spots, and (8) dilute nonagouti with white spots. These 8 types could represent as many as 27 different combinations of genes, considering only the characters mentioned. Examples of the effects of certain combinations of genes for color are given in the appendix (p. 1343). In many cases there are no data on the results to be expected from given combinations.

This illustrates the fact, well known to geneticists, that often the only way to judge what an animal does carry in its inheritance is by a sufficiently extensive progeny test.

Genetic studies indicate that color, type of hair, length of legs, form of head and body, and many other characters can be transferred from one breed to another by cross-breeding. It is undoubtedly by cross-breeding followed by selection that much of the variation in dogs has come about. New mutations—sudden changes in the germ plasm, later passed on in inheritance—were undoubtedly transmitted to different breeds by cross-breeding and greatly increased the number of types. The large number of types in turn allowed great leeway for selection and the development of still different forms. Many mutations are decidedly disadvantageous to the animals possessing them—so much so that under wild or primitive conditions they may not survive. Under the conditions of domestication, however, many of the mutant types not only survive, but may be superior for certain of man's uses. For example, certain inherited characters possessed by the Russian Wolfhound give him greater speed than the wolf so that he is useful for hunting wolves. On the other hand it is doubtful whether the Russian Wolfhound could compete successfully with the wolf in the wild state because he possesses certain other inherited characters that would put him at a disadvantage, such as a less well-developed sense of smell and a type of intelligence that is not quite so well adapted to self-preservation as that of the wild animal. Reports (*5, v. 1, p. 38*) of dogs that have returned to the wild state—feral dogs—indicate that their descendants are often wolflike in form.

MEASURING THE ABILITY OF DOGS IN COMPETITION

If one were to undertake a comprehensive genetic program on the inheritance of many of the characters that make dogs useful, a system of measurements of these characters would have to be worked out so that accurate comparisons could be made. At the present time dogs are used in competitive trials of various kinds, out of which certain measurements have been developed. Generally, however, these tests are of a sporting nature and chiefly measure the ability of the animal to win over its opponents under the particular conditions of the trial.

[5] Dominance probably would not be complete in all cases so that it might be possible to subdivide some of the phenotypic classes.

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Often they measure several distinct characteristics. Thus a winning combination must generally include a strong desire on the part of the dog to succeed, excellent morphological and psychological adaptability, a high degree of coordination of physical and mental powers and often a high degree of intelligence, and perfect cooperation between the dog and his trainer or handler. While such things are often only crudely differentiated or measured in competitive trials, nevertheless, such trials have been a very important factor in the development of breeds especially suited to certain types of competition. The following brief descriptions are given to illustrate what has been done in this connection as well as because of their general interest to dog breeders.

Track and Sled Racing

Dog racing has been on the increase in the United States since the devising of a mechanical rabbit for the dogs to chase. The first track using this invention was opened in 1919 in California. In 1935 meets were held in Arizona, Arkansas, California, Florida, Massachusetts, Minnesota, New York, Ohio, Oregon, Pennsylvania, Texas, and Washington. American racing records taken from the All Sports Record Book (*42*) are given in table 1

Table 1.—*American racing records of Greyhounds*

Distance (mile)	Dog	Time	Place and date
		Seconds	
3/16	Kiowa	18½	Tulsa, Okla , 1920
¼	Damon Runyan	25	Miami, Fla , 1927
¼ [1]	Swift and Sure	26⅘	Milwaukee, Wis , 1927
Futurity [2]	Karl Kelly	28	New Orleans, La , 1927
Do [1]	Domestator	29⅗	West Jefferson, Ohio, 1931
5/16	Oh Boy	31⅖	Miami, Fla , 1924
⅜	Altcar Drain	38⅗	New Kensington, Pa , 1930
7/16	Midnight Joe	45⅗	Miami, Fla , 1925
½	Red Skipper	52⅕	Belmont, Calif , 1932

[1] Handicap [2] Futurity is 55 yards longer than ¼ of a mile

These records are not quite so fast as the best time reported for running horses on oval tracks—three-eighths of a mile in 33½ seconds, seven-sixteenths of a mile in 39 seconds, and one-half mile in 46⅕ seconds. Mick the Miller, a British dog, considered the world's fastest Greyhound, has a record of 600 yards (a little less than three-eighths of a mile) in 34 seconds, which compares very well with the best running-horse record for approximately the same distance. Perhaps a clearer idea of how fast this dog was traveling may be gained from stating the rate as an average of 36 miles per hour for a distance of 600 yards.

According to Menke (*42*), Mick the Miller is said to be the most intelligent of greyhounds and showed uncanny ability in getting clear of "jams" in the running of races, thus giving him undisputed passageway. From 1929 to the end of 1931 he won $50,000 in purses and numerous cups and trophies. He was 9 years old in 1935, retired and quartered at Walton-on-Thames for breeding purposes even though his exact ancestry was unknown. The increase of track racing in this country has resulted in the importation of thousands of Greyhounds

from England and Ireland and the crossing of these dogs with American Greyhounds.

Another form of racing requiring a very different type of dog is dog-sled racing. The most famous of these races are run in Canada and Alaska—for example, the Eastern International Dog Sled Derby run annually over a 120-mile course at Quebec; the Hudson Dog Sled Derby (generally called The Pas Derby) run over a 200-mile course from The Pas, Manitoba, to Flin Flon and return; and the All-Alaska Dog Race at Nome. Similar races have been run in New Hampshire, in upper New York State, and from Winnipeg, Manitoba, to St. Paul, Minn. As the races are run on scheduled dates regardless of the weather, there is considerable variation in the time required by the winning teams. Thus, over the 200-mile course at The Pas Derby the time has varied from 24 hours 51 minutes in 1922 to 37 hours in 1929. Alaska's Borden marathons run over a course of 26 miles 385 yards, has been won in time varying from 1 hour 50 minutes 27 seconds to 3 hours 35 minutes. Albert Campbell, a Cree Indian, drove his team of six dogs 522 miles in 118 hours 16 seconds to win the Red River International Derby from Winnipeg, Manitoba, to St. Paul, Minn. Rules governing the contests vary with regard to the number of dogs allowed per team, whether the race must be run in laps, and other points.

Because of their remarkable strength and endurance, Huskies have been very successful in these dog-sled races. These dogs are the result of crossing Eskimo dogs, which probably have considerable wolf inheritance, with such breeds as Great Dane, Newfoundland, or German Shepherd. It may well be that at least a part of their superiority in strength and endurance is an expression of hybrid vigor. Deerhounds have been used in recent years in crosses with the Eskimo dogs, but though the offspring are big, rugged animals, it is said that temperamentally they are more of a hunting-dog than of a sled-dog type and so are not such useful draft animals as some of the other cross-breds. Greyhounds are also said to have been tried in crosses with the Eskimo dogs. The offspring have superior speed but lack the ability to withstand the severe climatic conditions under which the sled races are often run. Today it is hard to find pure Eskimo dogs in the North as the Eskimos themselves prefer the stronger cross-breds.

Hunting and Herding Field Trials

Field trials for dogs are now widely held in the United States and in some other countries, notably England, to test the ability of bird dogs such as Setters and Pointers. These trials are actual hunting contests in which the dogs are scored by judges for their ability to locate the birds by scent, to point in the direction of the game, to hold the point until the hunter fires at or flushes the birds, to retrieve the game when crippled or killed, to cover a large area both rapidly and efficiently, and to demonstrate endurance, tractability, style, and perseverance. Generally the competition is divided into three classes, puppy, derby, and all-age, the division depending on the age of the dog. Contestants are run either singly or in pairs.

Similar trials are also being run for Retrievers and Spaniels. In these, the animals must work both on land and in the water and more

attention is paid to retrieving the game and less to pointing. Field trials with Foxhounds, Bloodhounds, and other types of sporting dogs, as well as ratters, are sometimes held, and there seems to be a growing interest in them.

One of the effects of these trials has been a decided tendency to develop two strains within some of the breeds involved, one being bred to meet the requirements of field trials and the other to meet bench-show requirements of the fancier or the standard set up by the breed association. In the first strain, mental aptitudes and physique are stressed, and in the second, body conformation and color. A good example of this is to be found in English Setters, in which the Llewellin strain has been very successful in the field, while the Laverack strain has been most noted on the bench.

The herding of sheep by dogs goes back to prehistoric times, though, of course, organized sheep dog trials such as are held today in a number of countries to determine the ability of the dogs in competition are of comparatively recent origin. In Germany organized trials were held about the beginning of the present century. In 1873 the first sheep dog trial was held in Wales. Since the World War, these trials have become very popular in Great Britain and are also held on a large scale in Australia. In the United States for the last 9 years a sheep dog contest has been held annually in New England and exhibitions are given at a number of fairs and livestock shows.

So far the trials in the United States have been of the type held in Great Britain. One dog is run at a time and is directed entirely with whistles and gestures by the master. Scores are given for the manner and style with which the dogs handle the sheep. Trials are held in a meadow, with the sheep being liberated at one end while the dog and shepherd enter at the other. The dog is then sent out to gather in the sheep, which he must bring to the shepherd. Then he must drive them through a number of hurdles and finally into a small pen in the open field. In some contests the dog is also required to cut out or "shed" a certain number of marked sheep from the flock. All of this must be done within a certain time limit, without hurrying the sheep, and always with complete obedience to the shepherd's commands.

Practically all the dogs entered in the contests in Great Britain or the United States are Border or Working Collies. These dogs generally have long black and white coats and are somewhat smaller than the Collies seen at dog shows. Their heads also are somewhat broader and shorter than those of the show Collies, which have been selected for long, flat, narrow-type skulls. Scotch and English shepherds train their dogs not to bite the sheep but only to bluff them, while in Germany, where the dog must often protect the crops from the sheep, the shepherds train the dogs to grip the sheep if necessary. Border Collies seldom bark, which is an advantage under the conditions prevailing where they ordinarily are used. In brush country, however, a barking dog can be heard by the sheep when he cannot be seen and is thus often more successful in his work than a quiet one. In some countries, the sheep must be protected from wolves and other wild animals so that large and powerful dogs are needed. Because of these differences in requirements and training, it is not to be expected that

the more than 40 varieties of herding dogs, including such varied breeds as the German Shepherd, Aftscharaka, Kelpi, Puli, Old English Sheepdog, Komondor, Bundas, Riesenschnauzer, etc., can compete satisfactorily in trials designed for the Border Collie alone.

In former years some breeds of dogs were bred to fight each other in the pit or arena or, as in bullbaiting, to fight a bull. This kind of competition has largely been outlawed, and the fighting breeds—Bull Terriers, Bulldogs, and Boxers—are now kept largely as companions and guards.

Some of the recent dog shows have been featuring a new type of contest called an obedience trial in which prizes are awarded on the obedience of each animal to a number of commands. Poodles have been outstandingly successful in these competitions.

Dog Shows

Of the organized competitive activities connected with dogs, the dog shows attract the most interest. In 1935 there were, according to Menke (*42*), 2,760 bench shows in the United States, with 200,000 entries and 1,000,000 paid admissions. No one knows how many dogs there are in the United States, though a rough estimate would be between 10,000,000 and 12,000,000. There were registered with the American Kennel Club in the single year of 1935, 72,000 dogs that were eligible for shows.

The largest dog show in the United States, the Westminster Dog Show held in Madison Square Garden, New York, N. Y., had a record in 1935 of 2,837 entries with 85 breeds represented. This was the fifty-ninth Westminster Dog Show held under the auspices of the American Kennel Club and it drew entries from all over the world.

As is the case with other domestic animals, the dogs that can win highest honors in competition either in field trials or bench shows, usually attract the breeders, and dogs that can transmit their ability to win soon become the foundation animals of a strain or breed. Thus the sires Gladstone and Count Noble, which produced 25 and 30 field-trial winners, respectively, are to be found in the ancestry of most field-type English Setters in the United States. Dog shows also have been one of the most potent influences on breeding in the last half century. By fostering the adoption of breed standards and the use of these in judging they have kept before dog breeders fairly definite aims to be attained. They have also been a most efficient medium for advertising those animals that, in the opinion of the judges, were the best in their respective breeds and have helped to spread information and interest in dog breeding. The standards, of course, have often been largely influenced by changing fashions and frequently have little or no relation to utility.

On the whole this use of bench-show or field-trial winners as breeders has made for progress, although the overwhelming emphasis on individual performance has also sometimes perpetuated and spread through the breeds defects carried by the foundation stock. The ideal condition for the progress of the breeds would be to place the emphasis on breeding records, which should include all the offspring of a given animal instead of the winners only or at best the offspring

without serious defects. Thus breeders would have a progeny test that would indicate the real genetic constitution of a given animal.

The American Kennel Club (*3*), under whose auspices most of the dog shows are held, included descriptions and standards of 102 breeds of dogs in their book Pure-Bred Dogs published in 1935. These breeds, together with their color, size, and principal uses, for the most part as given in Pure-Bred Dogs, have been listed in table 3. This table clearly indicates the variety of dogs in the United States. It is impossible, however, to give an adequate amount of detail, and for more complete information the readers should consult the American Kennel Club's publication.

POSSIBILITIES OF FURTHER GENETIC RESEARCH WITH DOGS

The improvement of dogs along certain practical lines by the use of a knowledge of inheritance appears to offer definite promise for the future. Thus the relative number of German Shepherd dogs that are suitable as guides for the blind or for police or army work can be greatly increased by means of selective breeding and the application of genetics as has been demonstrated at Fortunate Fields (*22*). Also, working ability can be successfully combined to a considerable extent with show form according to the results obtained by the same organization.

Superior hunting dogs may be bred for certain conditions as was done by Adametz (see Iljin (*25*)), who crossed English Pointers to German Pointers to produce a rapid-working dog that could stand the heat on the steppes of Moravia.

Improved physical and disciplinary traits can probably be secured from certain crosses. Iljin (*25*) states that in several regions of the Union of Soviet Socialist Republics German Shepherd dogs and Doberman Pinschers are crossed for that purpose.

The histories of a large number of the present breeds as given by the American Kennel Club (*3*) indicate that they originated from matings between animals of two or more breeds made purposely to combine certain desirable characteristics in one strain.

Doubtless many abnormalities or defects, such as cryptorchidism, cleft palate, reduced larynx, certain types of periodic eczema, etc., can be eradicated or controlled through breeding as indicated by the work of Koch (*28*). Studies on the inheritance of resistance to infectious diseases with other species of animals, as the mouse, rabbit, guinea pig, and chicken (see Hill (*20*) for a review of the subject) would indicate that it may be possible to develop strains of dogs with high resistance to certain of the infectious diseases, such as distemper.

In addition to the improvements that might be made in the dogs themselves, undoubtedly studies of the inheritance of various characters in dogs would aid in a better general understanding of mammalian genetics.

That dogs have been used extensively in anatomical, physiological, and psychological research, as already indicated, but to a very limited extent in genetic research is probably due to a number of reasons. (1) Research workers in the fields mentioned have been able to utilize dogs from city pounds and cheap animals of nondescript breeding,

whereas in making a genetic analysis a large number of animals would have to be produced from specific matings. (2) In studying the inheritance of certain characters, notably psychological traits, for the study of which dogs are especially good subjects, methods of measuring many of the characters must first be perfected before genetic studies will be very fruitful. In the last analysis, however, probably the principal reason why less attention has been paid to genetic research with the dog has been the feeling that results promising greater immediate economic gain were to be had in other fields.

Yet within a single species dogs show so wide a range of intelligence and temperament that they are better adapted for studies of the inheritance of these characters with the crude methods now available than other species in which the differences are less marked, such as guinea pigs, rats, mice, rabbits, and poultry. Dogs also reproduce with reasonable rapidity and would not be so expensive to maintain in sufficient numbers under laboratory conditions as horses, cattle, sheep, goats, and swine. Thus the use of dogs as subjects in certain fields of genetic research appears to offer the most practical means of attacking certain very important problems.

Figure 4.—Puli bitch. One of four animals of this breed recently imported by the United States Department of Agriculture from Hungary for use in studying the inheritance of intelligence and related characters in animals. The Puli has the reputation of being an exceptionally good herding dog in its native country. The most favored colors are white, cream, gray, and black. Dogs weigh about 30 pounds, bitches about 25 pounds.

The Bureau of Animal Industry has just initiated a project to study the inheritance of intelligence and associated characters in farm animals with especial reference to the influence of such characters upon performance and production. Dogs are being used in the early phases of these studies because they probably exhibit a greater range in temperament and in intelligence than most animals; different breeds have been developed for widely different purposes and some of them have important agricultural uses.

In this project dogs of several breeds of different temperament will be subjected to certain tests to determine the range and type of intelligence and their suitability for various purposes, especially for the herding of sheep. Crosses also will be made between breeds and similar tests will be made on the offspring of the first generation and later generations following the cross. One of the breeds being studied is the Puli. Four individuals of this breed (fig. 4) were recently imported

by the Department from Hungary. These dogs are noted in their native country for their sheep-herding ability. Studies on this breed and its hybrids from crosses with several other breeds are now under way.

From these experiments facts will be secured on (1) the degree to which intelligence is inherited, (2) the manner of its inheritance, and (3) the influence of intelligence, temperament, and certain other psychological traits upon certain special aptitudes of the dog. The experiments will also furnish fundamental information on the type of temperament and psychological traits that are needed in dogs for special purposes. Furthermore, information will be secured on the relation of various types of temperament to such things as feed utilization, appetite, management, and growth. The results obtained from these experiments are expected not only to furnish information on these functions in dogs but also to be of value in pointing the way for further investigations of this nature with other farm animals.

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APPENDIX

CHARACTERS IN DOGS, THE INHERITANCE OF WHICH HAS BEEN STUDIED BY VARIOUS RESEARCH WORKERS [6]

Mental Aptitudes

Characters and breeds	Investigator
High head carriage of the English Pointer appears to be dominant to low head carriage of some strains of the German Pointers (a).[7]	Marchlewski (*41*).
High head carriage of bird dogs is dominant to low head carriage of Bloodhounds and Foxhounds (a).	Whitney (*64*).
Quiet style of hunting of the English Pointer appears to be dominant to the yelping style of some strains of the German Pointer (a).	Marchlewski (*41*).
Trail barking of hounds is dominant to still trailing of various breeds of mute trailers (a).	Whitney (*63*, *64*).

[6] It must be emphasized that many of the conclusions are tentative and that the phenotypic or outward expression of a character may in some cases differ decidedly as a result of differences in the environment or of various combinations and interactions of the gene or genes involved.
[7] Letters in parentheses indicate: (a) Author's statement, no data given, (b) conclusions drawn from small sample, (c) studbook records.

Mental Aptitudes—Continued

Characters and breeds	Investigator
Water-going propensity of the Newfoundland and bird dogs is dominant to lack of it in hounds (a).	Whitney (*64*).
Bird-hunting aptitude of bird dogs is imperfectly dominant to lack of it in hounds and other breeds (a).	Do.
Higher grades of pointing instinct appear to be incompletely dominant to lower grades in crosses of English Pointers and German Pointers (a).	Marchlewski (*41*).
The "backing" instinct is dependent on specific genes in crosses between English and German Pointers and strains of the same (a).	Do.
The active, almost nervous, temperament of the English Pointer is incompletely dominant to the more lethargic temperament of the German Pointer.	Adametz. (*See* Iljin (*25*).)
A factor inhibiting liveliness appears to be present in dogs. Thus the offspring of German Shepherd × Siberian are rarely lively. However, the situation is complicated as shown by the fact that the offspring of Doberman Pinscher × German Shepherd or of Doberman Pinscher × Airedale Terrier are often excitable (a).	Iljin (*25*).
Disposition showed a tendency toward segregation in the offspring from a cross of a very gentle and timid Old English Sheepdog to a playful aggressive Scotch Collie (b).	Gates (*16*).
Auditory undersensitiveness appears to be incompletely dominant to oversensitiveness in German Shepherd dogs. Probably more than one factor is involved.	Humphrey and Warner (*22*).
Tactual (body) undersensitiveness appears to be incompletely dominant to tactual oversensitiveness in German Shepherd dogs. Probably more than one factor is involved.	Do.
Both auditory and tactual sensitiveness appear to be associated with sex. Relatively more males are undersensitive and more females oversensitive than would be expected by chance.	Do.
Energy, distrust, willingness, and trailing willingness appear to be inherited, but evidence is not conclusive (a).	Do.

Body Characters Other than Color

Narrow pointed head of the sheep dog is dominant to the broad dished type of the Pointer (a).	Marchlewski (*41*).
Elongated type of head in the Greyhound is dominant to the Bulldog and Pug types of skull formation.	Stonhege and Wriedt. (*See* Marchlewski (*41*)).
Wide form of skull and lower jaw is dominant to narrow (as studied in the German Shepherd and crosses between the dog and the wolf) (a).	Iljin (*25*).
Head shape of the Boston Terrier and French Bulldog gives intermediate head shape when crossed with Dachshunds. Multiple factors are involved, some dominant and some recessive (a).	Stockard (*55*).
Head shape of English Bulldog is incompletely dominant to head shape of the Basset Hound (a).	Do.
"Brick"-shaped head of the Airedale Terrier is incompletely dominant to the type of the Doberman Pinscher (a).	Iljin (*25*).
Bulldog type of head is dominant to the head type of the Doberman Pinscher (a).	Do.
Short crown is dominant to long crown (a)	Do.
Head length shows intermediate type of inheritance (a)	Do.

Body Characters Other than Color—Continued

Characters and breeds	Investigator
The orbital angle [8] appears to be controlled by at least two factors in crosses between the German Shepherd dog and wolf. In the F_1 animals the angle is intermediate but closer to the dog type.	Iljin (*26*).
The form of the zygomatic process and maxillary angle (cheekbone and angle at its anterior end) appears to be controlled by at least two factors. Crosses were between the German Shepherd and the wolf. The F_1 animals were intermediate but closer to the wolf type.	Do.
Rotundity of the bullae ossea or ear bladders appears to be controlled by at least two factors in crosses between the German Shepherd dog and the wolf. The F_1's were intermediate.	Do.
Nonribbedness of the ear bladders appears to be controlled by at least two factors. Crosses between German Shepherd dog and wolf. F_1 intermediate but closer to wolf type.	Do.
Cheekbone breadth appears to be controlled by at least two factors. Blending type of inheritance.	Do.
Length of muzzle and head shape intermediate in offspring of normal-nozed Schnauzer-Dachshund × short-nosed Pekingese. Results from backcrosses indicate that the broad skull and greatly shortened muzzle of the Pekingese results from a single factor (b).	Wriedt (*67*).
Defective sight is associated with merle dilution (p. 1461) in the homozygous condition in Collies and with albinism in Pekingese	Mitchell (*43*); Pearson, Nettleship, and Usher (*49, pt. 2, pp. 460–520*).
Double nose is inherited apparently as an incomplete dominant in Siberians, Boxers, and Boxer × Bulldog (a).	Iljin (*25*).
Normal palate is a simple dominant to various types of cleft palate frequent in dogs with short skulls. The defect is due to a disturbance of the pituitary growth hormone (a).	Koch (*28*).
Normal larynx is dominant to reduction and narrowing of the larynx in Skye Terriers (a).	Do.
Pitch and timbre of the voice appear to be inherited, but there has been no analysis (a).	Iljin (*25*).
Yapping bark appears to be dominant to hound drawl (a).	Whitney (*63*).
Normal number of teeth is dominant to missing teeth in German Shepherds. Probably more than one factor is involved (a).	Humphrey and Warner (*22*).
Deafness is associated with homozygous merle dilution in Collies and with extreme white spotting in Great Danes and Bull Terriers.	Pearson, Nettleship, Usher (*49*); Mitchell (*43*).
Small ear size of Alsatian appears to be dominant to large ear size of the Pointer (a).	Marchlewski (*41*).
Triangular type of ear in English Pointer is dominant to the larger lobed type ear of the German Pointer (a).	Do.
Hanging or pendant ear carriage appears to be incompletely dominant to erect ears in Pointer × Alsatian and Ceylon Hairless × Dachshund.	Plate (*51*), Marchlewski (*41*).

[8] The angle formed by the intersection of a plane across the eye socket with a horizontal plane across the top of the skull.

Body Characters Other than Color—Continued

Characters and breeds	Investigator
Ear carriage appears to be generally due to three allelomorphs with the following relationships suggested: H^a semierect, H– lop, h– erect. H^a completely dominant to H or h. H incompletely dominant to h. H^aH^a – H^aH – H^ah – semierect Collie type. HH – lop. Hh – semierect. hh – erect.	Iljin (*25*).
There is also an independent semierect type of ear carriage as in the Russian Wolfhound, and an independent lop-eared type recessive to erect ear. No information is given on this last type (a).	Do.
Erect ear carriage seems to be partly dominant to faulty ear carriage in German Shepherds and probably depends on multiple factors (a).	Humphrey and Warner (*22*).
Narrow chest is dominant to broad chest (a)	Iljin (*25*).
Development of chest is intermediate in inheritance in crosses of English and German Pointers (a).	Marchlewski (*41*).
Dewlap in the German Pointer is dominant to lack of it in the English Pointer (a).	Do.
Body form in cross-breds from Doberman Pinscher × Rottweiler is intermediate.	Wriedt (*67*).
Body and trunk form of St. Bernard is dominant to that of Dachshund (b).	Lang (*34*).
Body and leg form showed segregation in a cross of Old English Sheepdog with Scotch Collie (b).	Gates (*16*).
Short tail or absence of tail is due to several factors apparently not related to sex (b).	Klodnitsky and Spett (*27*).
Short tail is dominant or incompletely dominant to long tail in Schipperkes, and Belgian or Brussels Griffons.	Iljin (*25*), Little (*38*).
Form and posture of the tail appear to be inherited in addition to length (a).	Iljin (*25*).
Homozygous short tail is lethal	Vilmorin. (*See* Wriedt (*66*)); Iljin (*25*).
Normal tail of Dachshund is dominant to screw tail of Boston Terrier or French Bulldog. Two factors appear to be involved (a).	Stockard (*55*).
Screw tail does not appear to be linked with bull-shaped head in crosses of the Boston Terrier or French Bulldog with Dachshund and in crosses of the English Bulldog with the Basset Hound (a).	Do.
Normal tail of the Basset Hound is a simple dominant over screw tail of English Bulldog (a).	Do.
Normal tail is a simple dominant to screw tail in the French Bulldog. Screw tail is apparently based on defective functioning of the growth hormone of the anterior lobe of the pituitary (a).	Koch (*28*).
Short legs of Dachshund, Basset Hound, Scottish Terrier, etc., are incompletely dominant to normal long legs of Saluki, Bull Terrier, French Bulldog, English Bulldog, Schnauzer, Fox Terrier, and other normal-legged breeds.	Lang (*34*); Stockard (*55*); Wriedt (*67*).
Catlike compact foot of the English Pointer appears to be incompletely dominant to open harelike foot of German Pointer (a).	Marchlewski (*41*).
Closed foot appears to be dominant to open foot in German Shepherd (a).	Humphrey and Warner (*22*).
Short foot appears to be dominant to long foot in German Shepherd (a).	Do.

Body Characters Other than Color—Continued

Characters and breeds	Investigator
Supernumerary (fifth) toe on the hind feet appears to be inherited in various breeds. Mode of inheritance has not been determined (a).	Iljin (*25*).
Short hair (S) is due to a single gene almost completely dominant to long hair (s) in the Newfoundland × Pointer, Belgian or Brussels Griffon, and Dachshund.	Lang (*34*); Anker (*4*); Iljin (*25*); Little (*38*).

Figure 5.—Haired and hairless Mexican dogs from the same litter. (Photograph by courtesy of the Journal of Heredity, after Stockdale (*1*).)

Rough or wire hair (R) appears to be due to a single gene incompletely dominant to smooth short hair (r) in Belgian or Brussels Griffons, Dachshunds, and Ceylon Hairless dog × Dachshund. The R series ($R-r$) interacts with the S series ($S-s$) to give the following phenotypes: RS and Rs=wire rS=short rs=long.	Plate (*51*); Anker (*4*); Iljin (*25*); Little (*38*).
In a cross of Old English Sheepdog with Scotch Collie, type of coat showed segregation with the additional appearance of short smooth coat. This indicates a more complex genetic basis for the inheritance of length of coat than shown above (b).	Gates (*16*).

Body Characters Other than Color—Continued

Characters and breeds	Investigator
Hairlessness (fig. 5) is due to a single gene incompletely dominant to normal hair in Mexican, Ceylon, African, and Egyptian hairless dogs and Ceylon Hairless × Dachshund. The gene appears to be lethal in the homozygous state and to be associated with defective teeth and often with a slender, greyhoundlike body conformation in the heterozygous individuals.	[Stockdale] (*1*); Plate (*51, 52*); Letard (*36*).
Cryptorchidism is inherited in many breeds. Normal descent of the testes is a simple dominant to cryptorchidism in breeds having pronounced head shortening and screw tail; apparently cryptorchidism is caused by defective functioning of the anterior lobe of the pituitary (a).	Koch (*28*).
Thyroid size is relatively larger in the offspring of Dachshund crossed to Boston Terrier than in either parent (a).	Vicari (*60*).
Relative size of thyroid in the German Shepherd is incompletely dominant to relative thyroid size of the Basset Hound (a).	Do.
Differences in structure of the thyroid found in various breeds appear to be inherited in Mendelian fashion (a).	Do.
The greater power of destruction of uric acid with the formation of allantoin found in most dogs appears to be dominant to the decreased ability reported in specimens of the Dalmatian breed (b).	Onslow (*45*).
Death of certain motor and sympathetic neurones in the lumbar region of the spinal cord causing weakness and paralysis of the hind legs and in the males chronic dilation of blood vessels to the erectile tissue appears to be caused by multiple genes. The hypothesis that three dominant genes must be present in order that the character be expressed is suggested by Stockard. This condition was observed by Stockard in crosses between St. Bernard and Great Dane, and between Bloodhound and Great Dane. It has been reported at times in purebred St. Bernards and Great Danes.	Stockard (*56*).
Estrual weakness [9] occurs as a dominant to its absence in many breeds of dogs. The defect is due to deficient functioning of the follicular hormone (a).	Koch (*28*).
One rut during the year is dominant to two ruts during the year in cross-breds from the wolf and dog (a).	Iljin (*26*).
A pleiotropic gene in the Dunker breed (dominant irregular spotting) affects color, eyes, general vigor, and the reproductive cycle in the female.	Wriedt (*66*).
Hypertrophy of the vaginal mucosa during heat, often leading to prolapse of the vagina, is probably dominant to the normal condition. It is especially frequent in families showing cryptorchidism and cleavage malformations and is apparently due to the imperfect functioning of the follicular hormone, the production of which is controlled by the sex hormone of the anterior lobe of the pituitary (a).	Koch (*28*).
Inherited periodic exzema is probably a simple dominant to its absence. Indications are that it is due to a thyroid disturbance (a).	Do.
Tendencies toward certain diseases, as cataract, whistling asthma, several forms of epilepsy, and recurrent inflammation of the eyes, appear to be inherited (a).	Iljin (*25*).

[9] The lack of readiness for copulation in the presence of normal morphological estrual phenomena.

Color Inheritance

Characters and breeds	Investigator
Color (C) appears to be a simple dominant to imperfect albinism (c^b) in the offspring of colored and albino Pekingese and in the progeny from albino Pekingese × black Pomeranians (Wright, using the data of Pearson, Nettleship, and Usher). Inconsistencies in the data are probably due to the interaction of other genes.	Pearson, Nettleship, and Usher (*49*); Wright (*68*); Pearson and Usher (*50*).
White coat with dark nose and eyes of white Pomeranian (c^d) appears to be a dominant allelomorph of partial albinism (c^b) (Cornaz albino, very pale grayish coat with pale-blue eyes appearing red in some lights) in the Pekingese (b).	Dawson (data from Pearson and Usher (*50*)).
The basic gene for color (C) is dominant to (c^r) which dilutes red to yellow (found in the Siberian) and to partial albinism (c^d) found in the Samoyede (a).	Iljin (*25*).
Intense color is incompletely dominant to a factor causing partial albinism (nearly white coat with grayish black nose and dark eyes) found in the Samoyede dog. In the heterozygous state recessive red is reduced to pale chamois while black is not affected (b).	Tjebbes and Wriedt (*59*), and data from Pearson and Usher (*50*).
Black (B) is a simple dominant to brown or liver (b) in Pointers, Cocker Spaniels, Dachshunds, Doberman Pinschers, Newfoundland × Pointer, and in crosses of wolf and German Shepherd dog.	Lang (*34*); Little (*37*); Barrows and Phillips (*6*); Wright (*68*); Anker (*4*); Iljin (*24*, *26*).
Yellow (A^Y), wild gray color (A) and black and tan spotting (a^t) appear to form an allelomorphic series. A^y restricts the distribution of black and is incompletely dominant over a^t. A^y and a^t are found in the Belgian or Brussels Griffon (b).	Little (*38*).
Sable is dominant to nonsable in Collies. It is due to a single gene (A^y) allelomorphic to the recessive bicolor or black and tan (a^t) and is in the agouti series. It is dominant to agouti or wild gray color (A) of the German Shepherd. Mitchell reports the following relationships: A^yA^y = clear yellow sable. A^ya^t = varies from almost a clear yellow to dark sable apparently governed by modifiers. A = agouti. A^ya = sable.	Mitchell (*43*).
Dominant black and tan (A^t), wild color (A), self-color (a), and recessive black and tan or liver and tan spotting (a^t) appear to form an allelomorphic series with dominance in the order given from crosses of Doberman Pinscher with a wolf, and Doberman Pinscher crossed to wild colored German Shepherds.	Iljin (*24*).
Wild gray, self-color, and black and tan appear to be present in an allelomorphic series in crosses of wolf and German Shepherd dog with dominance in the order given.	Iljin (*26*).
Dominant yellow and its allelomorph brindle are epistatic to all other color pigmentation except dominant black, common in Great Danes, sheep dogs, and certain breeds of terriers; also probably in the Bulldog and Mastiff, practically absent from breeds of Russian and French origin. (In the light of other evidence, it may be questioned whether dominant yellow and brindle are allelomorphs.)	Marchlewski (*41*).

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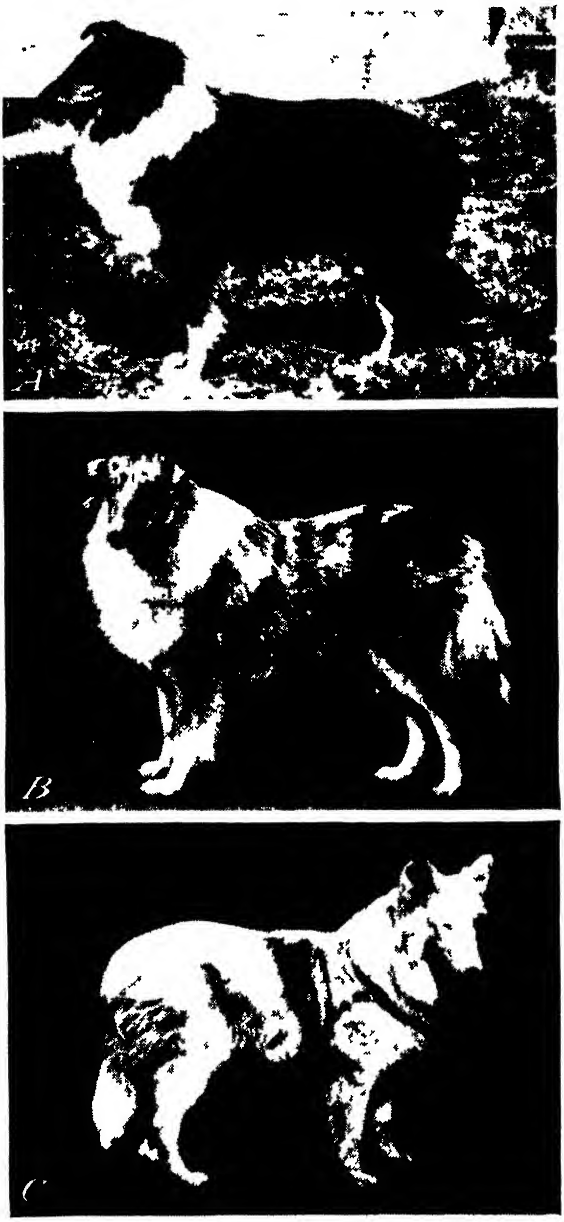
Color Inheritance—Continued

Characters and breeds	Investigator
Recessive black is hypostatic to dominant yellow but epistatic to brown (chocolate) and recessive yellow. It is also recessive to wild or wolf-gray color. Occurs in Irish Setters, Dachshunds, Liptaks, shepherd, and pastoral dogs (b).	Marchlewski (*41*).
Self-color (T)[10] is dominant to bicolor (black and tan) (t) in the Basset Hound and Dachshund. In combination with B=black and E=extension the (T–t) series gives: BET=self-black, BEt=black and tan. BeT =self-tan, red with black nose. Bet =red and lemon with black nose. Ibsen states bicolor is not in the agouti series but does not give evidence. (In the light of other evidence this may be questioned.)	Ibsen (*23*); Anker (*4*).
Solid color in incompletely dominant to bicolor (black and tan, brown and tan, red and lemon) in Cocker Spaniels, Doberman Pinschers, Collies, Gordon Setter × Irish Setter.	Barrows and Phillips (*6*); Iljin (*24*); Mitchell (*43*).
Dominant red is dominant to black and tan in Dachshunds.	Hagedoorn (*17*); Ibsen (*23*); Anker (*4*).
Yellow or red is epistatic to black and brown in Dachshunds.	Hagedoorn (*17*); Anker (*4*).
Red of Irish Terrier (probably (A^y)) is a simple dominant to black and tan of Fox Terrier or Welsh Terrier.	Hirschfeld (*21*).
Black and tan may be related to black in the following three ways: 1. The recessive factor by which it differs may be identical with factor by which red differs from black. A subsidiary factor is necessary to modify a red into black and tan. 2. Black and tan may be due to an allelomorph of the extension series. 3. Black and tan may be due to a factor independent of the extension series.	Wright (*68*).
Reddish brown (B) is epistatic to black (A) (except $AABb$=black) in Dachshunds and Ceylon Hairless crossed to Dachshund. Plate suggests the following: $AABB$=dark red. $AaBB$ and $aaBB$=light red. $AaBb$ and $aaBb$=yellow. $AABb$, $AAbb$ and $Aabb$=black. $aabb$=brown (c).	Plate (*51*); Anker (*4*).
Red appears to cover up the presence of agouti or "hare coloring" in the wire-haired Dachshund (c).	Anker (4).
Agouti is dominant to black and tan or brown and tan in the wire-haired Dachshund (c).	Do.
The more extensive tan markings in the Gordon Setter are partially dominant to the lesser tan markings (a).	Iljin (*25*).
Dominant black is epistatic to all other types of pigment formation and probably is an allel in the extension series. It is found in Pointers, Setters, Great Danes, Spaniels, and in some of the terriers, as the Fox Terrier (b).	Marchlewski (*41*).
Extension of black pigment (E) is dominant to restriction of black pigment; i. e., yellow (e) in Pointers (c).	Little (*37*).

[10] The symbol T used by Ibsen and Anker is not the same as that used in table 2 where bicolor is placed in the agouti series and T is used as the symbol for the ticking series.

Color Inheritance—Continued

Characters and breeds	Investigator
Black (E) is dominant to brindle (E^1) and to red or fawn (e). Brindle (E^1) is dominant to red or fawn (e) in Great Danes and Greyhounds. Little and Jones, and Warren suggest that they form a triple allelomorphic series (c).	Little and Jones (*39*); Dighton (*12*); Warren (*61*).
Brindling appears to be dominant to the lack of it in Irish Wolfhounds and Great Danes (c).	Darling and Gardner (*11*); Little and Jones (*39*).
Black or liver is a simple dominant to red (*ee*) (a)	Wright (*68*).
Black appears to be dominant to tan or red in the Doberman Pinscher.	Iljin (*24*).
Black and liver are dominant to recessive yellow present in Pointers, and frequently in English Setters (a).	Marchlewski (*41*).
Dirty-white belt, yellow-brown belt of medium intensity, and bright-yellow belt in wild gray hair appear to be determined by triple allelomorphic genes in crosses of the wolf and German Shepherd dog. Dominance tends to be in the order given but is very weak between the first two.	Iljin (*26*).
Grayish-white dappling, light-yellow dappling, red dappling, appear to be present in an allelomorphic series in crosses of wolf and German Shepherd dog. Dominance is in the order given.	Iljin (*26*).
Intense coat color is a simple dominant to a factor diluting black coat color to blue and red to fawn or lemon in Cocker Spaniels, Great Danes, Doberman Pinschers, and Greyhounds. In Greyhounds, Warren found some evidence indicating the factor diluting red was not the same as the one diluting black.	Barrows and Phillips (*6*); Little and Jones (*39*); Dighton (*12*); Warren (*61*); Iljin (*24*).
The rough hair gene appears to dilute the coat colors, especially yellow, in Belgian or Brussels Griffons.	Little (*38*).
Intense pigmentation of hair, ball of foot, claws, and skin in hairless dogs (D) is incompletely dominant to dilute pigmentation of same (d) in crosses of the Ceylon Hairless dog × the Dachshund.	Plate (*51*).
Dominant irregular white spotting harlequin pattern, often associated with wall eye and in extreme white individuals with deafness, is reported to be a simple dominant to the absence of such spotting in Cocker Spaniels, Great Danes, Old English Sheepdogs, Dalmatians, and possibly Bull Terriers. Though reported as a dominant, most individuals affected appear to be heterozygous. Iljin reports that this spotting pattern does not show when present in yellow or lemon hounds.	Pearson, Nettleship and Usher (*49*); Barrows and Phillips (*6*); Wright (*68*); Little and Jones (*39*); Wriedt (*65*); Marchlewski (*41*); Iljin (*25*); Humphrey and Warner (*22*); Mitchell (*43*).
Dominant irregular spotting (merle dilution—fig. 6) often associated with wall eye is reported to be due to a single gene dominant to the absence of such spotting in the merle Collie, dappled Dachshund, and Norwegian Dunker Hound. In the heterozygous condition it produces irregular dark spots on a lighter pigmented ground color. With yellow or sable animals, however, its presence is often difficult to detect unless it has affected the eyes. In the homozygous condition it produces pale-gray or yellow spots on a white coat and generally defective sight and hearing. Mitchell suggests the above pattern is produced by the same gene as the harlequin pattern except that in the latter case there is an independent modifying gene which dilutes the ground color to white.	Wriedt (*65*); Anker (*4*); Mitchell (*43*).



Collies showing the effects of the genes *V–v* for dominant spotting (merle dilution): *A*, Normal black and tan Collie (*vv*); *B*, blue merle Collie (*Vv*), which happens to have both eyes normal, but often one or both eyes will be wholly or partly of a pale bluish-white color—"wall-eyed"; *C*, merle Collie with defective sight and hearing (*VV*). Since blue merles or sable merles are mixed (*Vv*), they will not breed true when mated together. (Photographs by courtesy of the Journal of Heredity, after Mitchell (43).)

Figure 6.

Color Inheritance—Continued

Characters and breeds	Investigator
Self-color (S) is dominant to piebald white spotting (s) in hounds, sheep dogs, Doberman Pinschers, Great Danes, Cocker Spaniels, Newfoundland×Pointer, Ceylon Hairless×Dachshund, Airedale×Fox Terrier, and wolf×German Shepherd dog. It appears to be subject to modifying genes causing it to range from a very little white on the coat to practically entirely white animals. The lesser degrees of piebald white spotting appear to be dominant to the greater degrees. Haldane attributes this variation to three allelomorphic factors, s_1, s_2, and s_4. Wriedt suggests Ss animals are generally solid color except for small white markings on chest and toes.	Lang (*34*); Wright (*68*); Little and Jones (*39*); Wriedt (*65*); Plate (*51*); Warren (*61*); Haldane (*18*); Marchlewski (*41*); Iljin (*24, 25, 26*); Hirschfeld (*21*); Mitchell (*43*).
Self-color with white on chest and toes completely dominant over markings in Newfoundland×Pointer.	Lang (*34*).
Dominant white (W) is dominant to color (w). It occurs in the Russian Shepherd and sometimes in the Siberian (a).	Iljin (*25*).
Colored coat (W^1) appears to be a simple dominant to white coat (w^1) in Collies. Heterozygous animals (W^1w^1) often have more prominent white markings than those free of the factor. These white Collies have dark eyes and nose. As a rule there is some color on the head (a).	Mitchell (*43*).
Tricolor is caused by a combination of black and tan (bicolor, a^t) and piebald white spotting (s) in hounds and Collies.	Ibsen (*23*); Wright (*68*); Mitchell (*43*).
Pigmented point in the midst of a white area on top of the head usually dividing the pigmented auricular regions behaves as a dominant to the lack of it in Pointers (a).	Marchlewski (*41*).
Self-color of ear appears to be dominant to white spots on the ear. In the heterozygous condition there are a few white hairs on the ear (a).	Do.
Ticking or roan (fig. 7) is a simple dominant to the lack of it in Cocker Spaniels, Setters, Pointers, and Foxhounds. It does not show except on white, and heavier grades appear to be dominant to the lighter grades.	Barrows and Phillips (*6*); Wright (*68*); Whitney (*62*); Marchlewski (*41*).
Nonsilvering appears to be a simple dominant to silvering in Doberman Pinscher (a).	Iljin (*24*).
Eye color showed segregation in a cross of a dark brown-eyed Old English Sheepdog with a light brown-eyed Scotch Collie with the additional appearance of "wall eye."	Gates (*16*).
Dark eyes appear to be dominant to lighter colored ones in Cocker Spaniels and German Shepherds (a).	Barrows and Phillips (*6*); Humphrey and Warner (*22*).
Brown or yellow eyes (Y) appear to be dominant to blue eyes (y) (a).	Iljin (*25*).
Normal eyes (P) appear to be dominant to ruby eyes (p^r) (a).	Do.
Wall eye is associated with merle dilution in Collies, Old English Sheepdogs, Shetland Sheepdogs, Dappled Dachshunds, and Norwegian Dunker Hounds, and with irregular black and white spotting in harlequin Great Danes, Dalmatians, and Bull Terriers.	Gates (*16*); Pearson, Nettleship, and Usher (*49*), Anker (*4*); Wriedt (*65*); Mitchell (*43*).
The nose is always the same color as the footpads in Cocker Spaniels.	Barrows and Phillips (*6*).
The colors (black, blue, red, fawn, white, brindle, or white spotting) do not appear to be linked with sex in Greyhounds.	Warren (*61*).
None of the colors appear to be linked with sex in the Dachshund.	Anker (*4*).

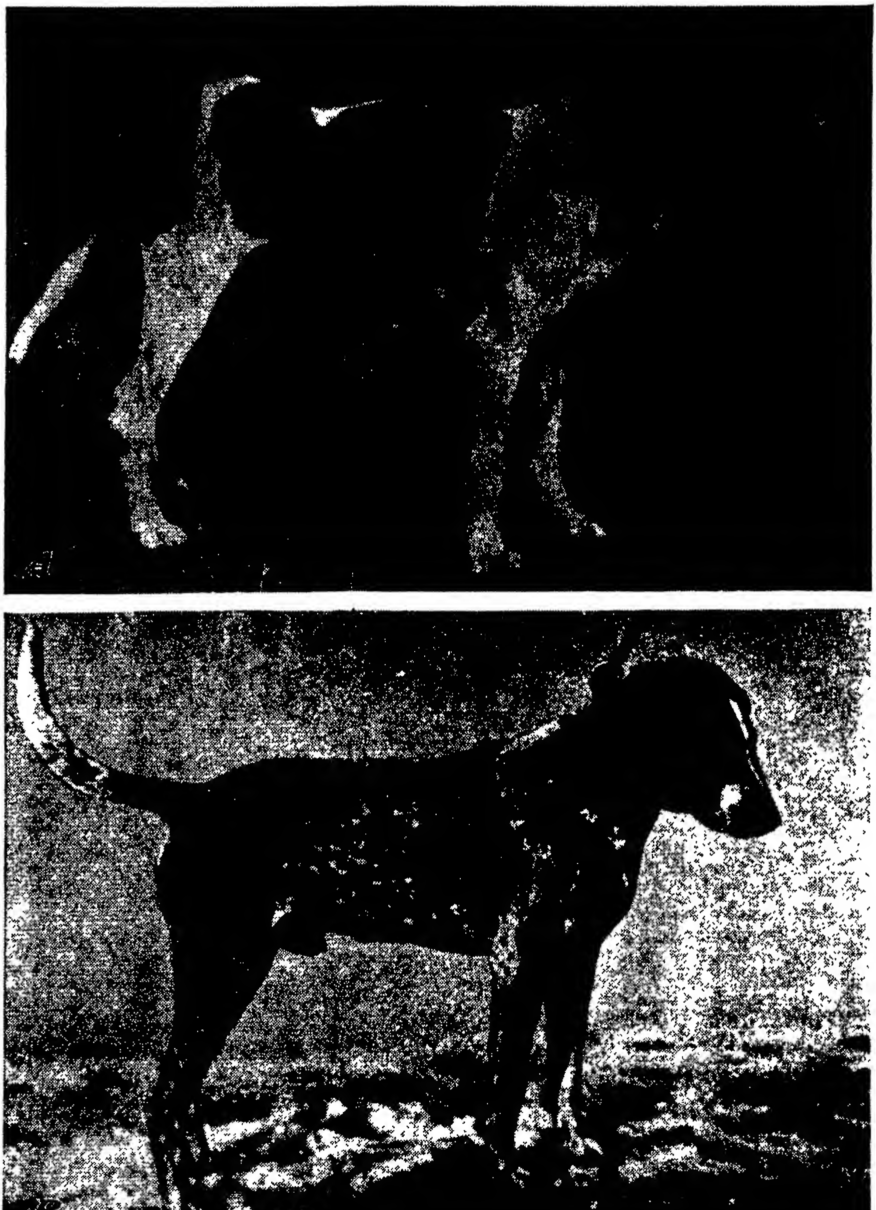


Figure 7.—Foxhounds showing the absence and presence of ticking, colored hairs intermingled with white hairs on those portions of the body that would otherwise be white: *A*, Foxhound bitch without ticking (*tt*); *B*, Foxhound dog with ticking (*Tt*). Eight of the fifteen offspring from the above animals were ticked. (Photographs by courtesy of the Journal of Heredity, after Whitney (*62*).)

TABLE 2.—*Allelomorphic color series in the dog* [1]

Series	Gene symbol	Phenotypic effect
C	C	Basic factor for color.
	c^r	Dilutes red to yellow (found in Siberians) may be Cc^d.
	c^a	Partial albinism, white coat, dark eyes and nose as in Samoyede and white Pomeranian.
	c^b	Partial albinism, slightly colored coat, blue eyes appearing red in reflected light, albino Pekingese.
B	B	Factor for black.
	b	Dilutes black of coat to chocolate or coffee brown and also dilutes nose and eye color.
A	A^y	Dominant yellow or sable.
	A	Wild gray, agouti.
	a	Self-color, black or nonagouti.
	a^t	Bicolor, black and tan, liver and tan, red and yellow.
E	E^D	Dominant black.
	E	Normal extension of black pigment.
	e^p	Partial extension of black pigment (brindle).
	e	Nonextension of black pigment, red or recessive yellow.
I	I	Dirty-white belts in wild gray hair.
	i^m	Yellow-brown (medium intensity) belts in wild-gray hair.
	i	Clear-yellow (intense) broad belts in wild gray hair.
I_1	I_1	Gray-white dapples.[2]
	i_1^m	Light-yellow dapples.[2]
	i_1	Red dapples.[2]
D	D	Intense color.
	d	Dilutes black to blue and possibly red to fawn or yellow.
V	V	Dominant spotting dilutes the coat and often the eye, nose, and footpads except for irregular pigmented areas, as in the merle Collie and harlequin Great Dane (apparently effected by modifiers).
	v	Self-color (in the absence of other genes for spotting).
S	S	Self or solid color.
	s	Piebald white markings (there may be other allels in this series).
W'	W'	Dominant white in Russian Shepherd dog and sometimes in the Siberian.
	w'	Colored.
W	W	Colored.
	w	White coat as found in Collies (possibly is an allelomorph of S or s with a modifier).
T	T	Ticking or roaning on white (there may be other allels in this series).
	t	Lack of ticking or roaning.
S_i	S_i	Nonsilvering.
	s_i	Silvering.
Y	Y	Brown or yellow eye color.
	y	Blue eye color.
P	P	Normal eye (greenish reflection).
	p^r	Ruby eye (red reflection).

[1] In general dominance within the series is in the order given. There is a divergence of opinion and lack of certainty with regard to the existence of some of the above genes and also with regard to the allelomorphic relationships (see list (pp. 1331-1341) and discussion in the text). The symbols have been changed in some cases from those used by the original investigator.

[2] Possibly the same as the I series; the different phenotypic effect may be due to different gene combinations.

FORMULAS FOR SOME OF THE MOST COMMON COLORS AND COLOR PATTERNS IN WORKING DOGS (HOMOZYGOUS INDIVIDUALS) [11]

Genetic formula	Phenotypic appearance
$CCAABBDDEESS$	Wild gray.
$CCaaBBDDEESS$	Black.
$CCaabbDDEESS$	Liver.
$CCaaBBddEESS$	Blue.
$CCaaBBDDe^pe^pSS$	Brindle.
$CCaaBBDDeeSS$ $CCAABBDDeeSS$	Yellow, black nose.
$CCaabbDDeeSS$	Yellow, brown, or light colored nose.
$CCa^ta^tBBDDEESS$	Black with tan markings.
$CCa^ta^tbbDDEESS$	Liver with tan markings.
$CCa^ta^tBBddEESS$	Blue with tan markings.
$CCaaBBDDEEss$	Black with white spots.
$CCaabbDDEEss$	Liver with white spots.
And generally c^dc^d W'	White—Thus c^dc^d and W' are epistatic to, or cover up the action of the other genes given.

[11] From Iljin (25) with slight modifications. He included in working dogs the following breeds: Doberman Pinscher, German Shepherd, Airedale Terrier, Rottweiler, Giant Schnauzer, Boxer, Siberian, shepherd dog of southern part of the Union of Soviet Socialist Republics. Because of the phenomenon of dominance, heterozygous individuals will often appear similar to homozygous ones; however, segregation may show up among the offspring of the former. Since there are many genes affecting color, animals heterozygous for at least some of them are quite common even among purebred dogs.

TABLE 3.—*Color, weight, and most important uses of breeds of dogs recognized by the American Kennel Club* [1]

GROUP 1, SPORTING DOGS

Breed	Principal colors	Weight		Principal uses
		Males	Females	
		Pounds	*Pounds*	
Wire-haired Pointing Griffon.	Steel gray with chestnut splashes. Gray white with chestnut splashes. Dirty white mixed with chestnut. Never black.	About 56	About 56	Pointing game birds; retrieving.
Pointer	White with liver, black, or lemon markings, solid black or liver.	50–55	45–50	Pointing and retrieving game birds; companions.
Short-haired German Pointer.	Solid liver, liver and white spotted, liver and white spotted and ticked, liver and white ticked.	55–70	45–60	Pointing and retrieving game birds, including ducks; trailing; companions.
Chesapeake Bay Retriever.	Dead-grass color, dark brown to faded tan.	65–75	55–65	Retrieving, especially ducks.
Curly-coated Retriever.	Black or liver	60–70	60–70	Retrieving game, land or water.
Flat-coated Retriever.	do	60–70	60–70	Do.
Golden Retriever.	Rich golden	65–68	55–60	Do.
Labrador Retriever.	Generally black	55–65	55–65	Retrieving and gun dogs.
English Setter	Black, white and tan, black and white, blue belton,[2] lemon and white, lemon belton, orange belton, liver and white, liver belton, solid white.	55–70	50–65	Pointing and retrieving game birds; companions.
Gordon Setter	Black with tan markings	About 70	About 70	Do.
Irish Setter	Golden chestnut or mahogany red.	50–65	40–55	Do.
Brittany Spaniel	Liver and white or orange and white. Often with roan ticking.	([3])	([3])	Pointing and retrieving.
Clumber Spaniel	Lemon and white, orange and white.	55–65	35–50	Finding game, especially birds; retrieving.
Cocker Spaniel	Solid black, red, or liver. Above colors with white on chest.	18–24	18–24	Finding game, especially birds in heavy cover; retrieving; companions.
English Springer Spaniel.	Any color except red and white, and lemon and white.	Average 45	Average 42	Finding and springing game, especially birds; retrieving.
Field Spaniel	Solid black, liver, golden liver, mahogany red, roan, or the above with tan over the eyes and on cheeks, feet, and pasterns.	35–50	35–50	Finding game, especially birds; retrieving.
Irish Water Spaniel.	Deep pure liver without white.	About 60	About 60	Retrieving ducks.
Sussex Spaniel	Rich golden liver	35–45	35–45	Finding game, especially birds in heavy cover.
Welsh Springer Spaniel.	Dark rich red and white	33–40	33–40	Finding game, especially birds in rough country with heavy cover; retrievers; companions.

[1] For more complete descriptions and histories of the various breeds see the American Kennel Club (3) from which most of this information was taken. An approximate weight to give the reader some idea of the size of the breed has been added, where possible, for those breeds having no official weight range in the breed standard. Dogs of all breeds are used as companions to at least some extent, even though that use is not listed for each breed in the table. The group classification is that used by the American Kennell Club. It is realized that in some respects this classification is not consistent with respect to the uses and characters of certain breeds. However, it would be difficult to make a classification that would not be subject to similar criticism, also the above classification appears to meet the needs of breeders fairly well.

[2] The belton color is produced by an intermingling of colored and white hairs in the coat.

[3] No published weights.

Table 3.—*Color, weight, and most important uses of breeds of dogs recognized by the American Kennel Club*—Continued

GROUP 2. SPORTING DOGS (HOUNDS)

Breed	Principal colors	Weight		Principal uses
		Males	Females	
		Pounds	*Pounds*	
Afghan Hound	Black and tan, black, golden	About 60	About 60	Coursing jack rabbits; in its native country, hunting gazelle and leopard.
Basset Hound	Generally black, tan or white, or a combination of these.	25–40	25–40	Hunting foxes, rabbits, and pheasants; trailing in dense cover.
Beagle	Black, tan, black and tan, black and white, tan and white, black and tan and white.	(3)	(3)	Hunting individually, or in packs for hare, rabbit, and drag hunting.
Bloodhound	Black and tan, red and tan, tawny, sometimes with small amounts of white.	90	80	Trailing criminals and hunting for lost persons and articles.
Dachshund, 3 varieties—smooth or short-haired; wire-haired; long-haired.	Solid red (tan) of various shades, black with tan points, chocolate with tan points.	5–35	5–35	Companions; hunting rabbits; in their native country hunting badger.
Scottish Deerhound.	Dark blue gray, darker and lighter grays, brindles, yellow and sandy red, red and fawn.	85–110	75–95	Hunting wolves, coyotes, rabbits; formerly for hunting deer in Scotland; companions.
American Foxhound.	Black, tan, black and tan, black and white, tan and white, black and tan and white, often ticked.	50–60	50–60	Fox hunting; drag hunting; used singly or in packs.
English Foxhound.	Black, tan, black and tan, black and white, tan and white, black and tan and white.	60–80	60–80	Fox hunting; drag hunting; generally in packs.
Greyhound	Black, blue, brindle, red, fawn, white and above colors with white.	65–70	60–65	Coursing hare and jack rabbits; racing.
Harrier	Black, tan, black and tan, black and white, tan and white, black and tan and white, sometimes of a blue mottled color.	About 56	About 56	Hunting hare and drag hunting.
Norwegian Elkhound.	Gray with black tips to the long covering hairs, somewhat lighter on under part of body.	About 60	About 60	Hunting big game; companions.
Otterhound	Blue and white, grizzle or sandy, black and tan.	Up to 65	Up to 65	Companions; formerly for hunting otter in England.
Saluki	Cream, fawn, red, grizzle and tan, black and tan, white and chestnut, tricolor (black, white and tan), solid black.	About 70	About 70	Coursing; hurdle racing; companions.
Whippet	Black, blue, red, white, fawn, gray, brindle, and combination of these with white.	10–28, average 20.	10–28, average 20.	Racing; coursing rabbits; companions.
Irish Wolfhound	Gray, brindle, red, black, pure white, fawn.	Minimum 120	Minimum 120	Running and killing coyotes and wolves; guards; companions.
Russian Wolfhound.	White usually predominating marked with lemon, tan, brindle, gray, or black.	75–105	55–90	Hunting wolves; coursing hare; companions.

[3] No published weights.

TABLE 3.—*Color, weight, and most important uses of breeds of dogs recognized by the American Kennel Club*—Continued

GROUP 3. WORKING DOGS

Breed	Principal colors	Weight		Principal uses
		Males	Females	
		Pounds	*Pounds*	
Alaskan Malamute.	Wolfish gray or black and white. Caplike or masklike marking on face.	65–85	50–70	Sledge dogs; dog-sled racing.
Belgian Sheepdog.	Long-haired variety, black. Short-haired variety, brindled fawn with black, mask.	About 53	About 53	Herding sheep; police and army service.
Bouviers de Flandre.	From fawn to black through pepper and salt, gray and brindle.	(3)	(3)	Farm dog; watchdog; police and army service.
Boxer	Fawn and brindle with mask, white with black, fawn or brindle markings.	About 50	About 50	Guards and watchdogs; police work; companions; formerly dog fighting and bull baiting.
Briard	Black, black with some white hairs, dark and light gray, tawny, and combinations of gray and tawny.	(3)	(3)	Sheep and guard dogs; police and army service.
Bull-Mastiff	Any shade of fawn or brindle.	115	100	Guards and watchdogs.
Collie (rough)	Black and tan with white frill and collar, sable with white markings, white, blue merle.	60	50	Herding or driving livestock; companions.
Collie (smooth)	Black and tan with white markings, sable with white markings.	60	50	Do.
Doberman Pinscher.	Black, brown, or blue with rust-red sharply defined markings.	65	75	Guards; watchdogs; police and army service.
Eskimo	Black, white, black and white, wolf gray, blue gray, all shades of tan or buff and all combinations of these colors.	65–85	50–70	Draft and pack service, especially on ice and snow; hunting in the Arctic.
German Shepherd.	Various shades of gray, black, black and tan, brindle, brown, white marking permitted.	About 55	About 55	Herding livestock; police and army service; watchdogs; guides for the blind.
Great Dane	Brindled, fawn, blue, black, harlequin.	120–160	100–130	Guards; companions; originally for hunting large game.
Great Pyrenees	White or principally white with markings of badger, gray, or tan.	100–125	90–115	Guards and companions; used for guarding flocks and for pack and draft service in the Pyrenees Mountains.
Kuvasz	Pure white	(3)	(3)	Guards and companions.
Mastiff	Silver fawn or dark fawn brindle, with muzzle, ears, and nose black.	About 170	About 170	Guards and companions; formerly for fighting (dog fighting, bull baiting, bear baiting, etc.).
Newfoundland	Dull jet black, white and black or bronze.	140–150	110–120	Water dogs; formerly for carrying life lines from stranded vessels; guards; companions.
Old English Sheepdog.	Gray, grizzle, blue or blue merled, with or without white markings in varying amounts.	About 65	About 65	Herding cattle or sheep; watchdogs; companions.
Rottweiler	Black with tan or brown markings.	(3)	(3)	Driving livestock; pulling carts; guards; police service.

3 No published weights.

TABLE 3.—*Color, weight, and most important uses of breeds of dogs recognized by the American Kennel Club*—Continued

GROUP 3. WORKING DOGS—Continued

Breed	Principal colors	Weight		Principal uses
		Males	Females	
		Pounds	*Pounds*	
Samoyede	Pure white, white and biscuit, cream.	About 45	About 45	Watchdogs; companions; sledge dogs and herding reindeer in Siberia.
Giant Schnauzer	Pepper and salt colored or similar equal mixtures, pure black or black and tan.	(3)	(3)	Police service; guards; formerly cattle driving.
Shetland Sheepdog.	Sable, black, blue, merle, marked with varying amounts of white and tan.	7-10	7-10	Watchdogs; sheep herding; companions.
Siberian Husky	White, black, gray, with white and black markings.	54-64	44-54	Sled dogs.
St. Bernard	Red, light or dark brindle, with white markings.	170-210	160-190	Guards; companions; rescue work at the Hospice of St. Bernard.
Welsh Corgis (Cardigan).	Red (sable, fawn, or golden), brindle, black and tan, black and white, blue merles.	18-25	15-22	Watchdogs; companions; driving cattle.
Welsh Corgis (Pembroke).	Any color other than pure white.	20-24	18-22	Companions.

GROUP 4. TERRIERS

Breed	Principal colors	Males	Females	Principal uses
Airedale Terrier	Head and ears tan, except for dark markings on each side of the skull, legs up to thighs and elbows tan; body, black or dark grizzle.	40-45	About 40	Guards; hunting; herding livestock; police and army service; companions.
Bedlington Terrier.	Dark blue, blue and tan, liver, liver and tan, sandy, sandy and tan.	24	22	Pets; formerly used on badgers, foxes, otter, etc.
Border Terrier	Red wheaten, grizzle and tan, or blue and tan.	13-15½	11½-14	Sporting terrier; bolting foxes.
Bull Terrier	White	12-60; average, 50.	12-60; average, 45.	Guards and companions; formerly for dog fighting.
Cairn Terrier	Any color except white, dark muzzle, ears and tail tip desirable.	14	13	Pets; killing vermin; formerly for bolting otter, foxes, and vermin.
Dandy Dinmont Terrier.	Pepper or mustard (dark bluish black to light silvery gray or reddish brown to pale fawn).	14-24	14-24	Watchdogs; companions; hunting and killing vermin.
Smooth and Wire-haired Fox Terrier.	Predominately white, black, tan or black and tan markings.	14-18	14-16	Watchdogs; companions; hunting and killing vermin; originally for bolting foxes.
Irish Terrier	Bright red, red wheaten, golden red.	27	25	Companions; hunting small game and vermin; house dogs; army service.
Kerry Blue Terrier.	Light to dark blue	33-38	32-36	Watchdogs; companions; hunting; shepherd dogs.
Lakeland Terrier	Blue, blue and tan, black and tan, red, mustard, wheaten, grizzle and black.	Not over 17	Not over 16	Watchdogs; companions; hunting small game.
Lhassa Terrier	Golden, sandy, honey dark grizzle, slate, smoke particolor, black, white or brown, dark tips to ears and beard an asset.	About 14	About 14	Watchdogs; companions; and pets.

[3] No published weights.

Table 3.—*Color, weight, and most important uses of breeds of dogs recognized by the American Kennel Club*—Continued

GROUP 4. TERRIERS—Continued

Breed	Principal colors	Weight		Principal uses
		Males	Females	
		Pounds	*Pounds*	
Manchester Terrier.	Black and tan	14-22	14-22	Pets; companions; hunting and killing vermin.
Miniature Schnauzers.	Pepper and salt or similar equal mixtures, light or dark, including red pepper, pure black, black and tan.	15	12	Do.
Standard Schnauzers.	All pepper-and-salt colored or similar mixtures; pure black or black and tan.	About 28	About 28	Watchdogs; companions; hunting and killing vermin.
Scottish Terrier	Steel or iron gray, brindled or grizzled, black, sandy, or wheaten.	18-20	18-20	Pets; companions; originally for bolting foxes and other vermin.
Sealyham Terrier	All white or with lemon, tan or badger markings on head and ears.	21	20	Pets; companions; originally for hunting fox, otter, and badger underground.
Skye Terrier	Dark or light blue, or gray or fawn with black points.	16-20	14-18	Pets; formerly for bolting foxes.
Welsh Terrier	Black and tan or black grizzle and tan.	20	20	Companions; hunting fox; otter; badger and small game.
West Highland White Terrier.	Pure white	15-19	13-17	Companions; hunting vermin.

GROUP 5. TOY DOGS

Breed	Principal colors	Males	Females	Principal uses
Chihuahua, short and long coated.	Any color, solid or marked or spashed.	1-6	1-6	Pets; ratters.
English Toy Spaniel:				
King Charles or Black and Tan.	Black with tan markings	9-12	9-12	Pets and companions.
Ruby	Chestnut red	9-12	9-12	Do.
Blenheim	White with bright rich chestnut or ruby red markings, evenly distributed in large patches, spot on forehead.	9-12	9-12	Do.
Prince Charles or Tricolor.	White with black and tan markings.	9-12	9-12	Do.
Griffon:				
Brussels (wirehaired).	Reddish brown, a little black at whiskers and chin.	Small-sized, not over 7; large-sized, not over 12.	Small-sized, not over 7; large-sized, not over 12.	Do.
Belgian (wirehaired).	Black and reddish brown mixed black mask and whiskers.	do	do	Do.
Brabancons (smooth-coated).	Reddish brown, black with reddish brown markings.	do	do	Do.
Italian Greyhound.	All shades of fawn, red, mouse, blue, cream and white.	Lightweight, 8 and under; heavyweight, over 8.	Lightweight, 8 and under, heavyweight, 8 and over.	Do.
Japanese Spaniel	Black and white, all shades of red and white.	Lightweight, 7 and under; heavyweight, over 7.	Lightweight, 7 and under; heavyweight, over 7.	Do.
Maltese	Pure white	Not over 7; under 3, ideal.	Not over 7; under 3, ideal.	Do.

TABLE 3.—*Color, weight, and most important uses of breeds of dogs recognized by the American Kennel Club*—Continued

GROUP 5. TOY DOGS—Continued

Breed	Principal colors	Weight		Principal uses
		Males	Females	
		Pounds	*Pounds*	
Mexican Hairless	Skin generally slatey gray, sometimes mottled with flesh-colored spots.	About 14	About 14	Pets and companions.
Pappillon	Unicolor—any pure color. Two-colored—any color, with white. Tricolored—any two colors with white.	Less than 9	Less than 9	Do.
Pekingese	Red, fawn, black, black and tan, sable, bridle, white and particolor well defined, black masks and spectacles desired.	Maximum 14	Maximum 14	Do.
Pinscher (miniature).	Lustrous black with tan, rust red or lemon markings, solid yellow, solid red or stag red, solid brown or brown with red or yellow markings, solid blue or blue toned with red or yellow markings.	5–10	5–10	Do.
Pomeranian	Black, brown, chocolate, red, orange, cream, orange sable, wolf sable, beaver, blue, white, and particolors.	Lightweight, not exceeding 7; heavyweight, over 7.	Lightweight, not exceeding 7; heavyweight, over 7.	Pets; companions; watchdogs.
Pug	Silver or apricot fawn, with dark mask, black.	14–18	14–18	Companions.
Toy Manchester Terrier or Toy Black and Tan Terrier.	Jet black with rich mahogany tan markings.	About 7	About 7	Pets; companions; ratters.
Toy Poodle	Any solid color	Under 12	Under 12	Pets; companions; trick dogs.
Yorkshire Terrier	Dark steel blue with tan markings.	$2\frac{3}{4}$–13	$2\frac{3}{4}$–13	Pets and companions.

GROUP 6, NONSPORTING DOGS

Breed	Principal colors	Males	Females	Principal uses
Boston Terrier	Brindle with white markings, black with white markings.	Lightweight, under 15; mediumweight, 15–20; heavyweight, 20–25.	Lightweight, under 15; mediumweight, 15–20; heavyweight, 20–25.	Companions.
Bulldog	Red brindle, other brindles, solid white, solid red, fawn, or fallow, piebald.	50	40	Companions; guards; formerly for dog fighting and bull baiting.
Chow Chow	Any clear color, usually red, black, or blue.	55–60	55–60	Companions, pets and guard dogs. In China as sporting dogs.
Dalmatian	Ground color, pure white with small black or liver-colored spots scattered over the entire animal.	35–50	35–50	Companions, sport, formerly as coach dogs.
French Bulldog	All brindle, fawn, white, brindle and white.	Lightweight, under 22; heavyweight, 22–28.	Lightweight, under 22; heavyweight, 22–28.	Companions and watchdogs.
Keeshonden	Wolf gray	About 40	About 40	Do.
Poodle	Any solid or even color	Large, over 20; miniature, 12–20.	Large, over 20; miniature, 12–20.	Companions, pets, trick dogs, retrieving, watchdogs.
Schipperke	Solid black	Up to 18	Up to 18	Watchdogs, ratters, pets, and companions.

THE BREEDING OF TURKEYS

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THE chief problems of the turkey industry in its rapid development in the past have centered around feeding, management, and disease control. While advances have been made in these fields there is much yet to be learned, for new problems continue to arise. Breeding problems have received less study up to the present, partly because they have been crowded out by these other considerations, and partly because the turkey stocks of the United States have in a great measure fulfilled their purpose, which was to produce a superior meat product.

PRESENT NEEDS IN TURKEY BREEDING

BUT this situation will not necessarily hold forever and today both breeders and scientists are beginning to think about turkey-breeding problems. From the standpoint of the geneticist and the practical breeder, the desirable breeding objectives today might be summed up as follows:

1. The production of smaller size strains of turkeys to meet the growing demand for a family-size bird.
2. The improvement of body type to provide a higher proportion of edible meat, especially on legs and breast.
3. Early maturity in reaching market condition.
4. Higher egg production.
5. Higher fertility and hatchability.
6. Greater viability—that is, a lower mortality rate from various causes, including disease.

Constructive breeding methods can and should play an important part in reducing costs by considering these six objectives.

The breeding achievements of the past have consisted mainly of the production of color variations, a substantial increase in body weight and egg production, and a reduction in the length of legs and neck.

At present, for reasons that will be discussed later, there is a definite trend toward breeding a smaller, more efficient, more rapidly growing turkey. The main objective is a live bird weighing approximately 7½ to 10 pounds as a young hen or 11 to 15 pounds as a young tom, to meet the increasing popular demand for a well-matured small turkey. It might be thought that this demand could be supplied by selling turkeys at an early age when they average 8 to 15 pounds in weight. However, turkeys at this weight are continuing their rapid growth and they have too much "framework" and too little flesh. The real

object in breeding is to develop a small turkey that will be as plump and well grown as present-day turkeys are at Thanksgiving or Christmas time. A young tom of the small type is shown in figure 1.

The mortality of growing turkeys is a pressing problem and it is one that the breeder can materially assist in solving Turkey breeders, especially those that trap-nest their stock, can decrease these losses to a considerable extent by breeding from large families and from families whose progeny have had comparatively little mortality.

Figure 1 —A young small-type turkey tom, the second-generation product of a Bronze-White Holland cross. At 24 weeks of age this bird weighed 13 5 pounds, had a broad well-meated breast, and graded U. S. Prime. His keel measured 6 2 inches long and his shank 7.1 inches.

Egg production is an important factor in determining profit or loss in turkey-breeding work Turkey eggs are sold for hatching purposes by the producer for 10 to 50 cents each, depending on locality and breeding. Hence any increase in egg production will help profits considerably because it results in lowering the overhead and feed costs of producing hatching eggs In addition, turkeys are seasonal producers of eggs. They lay at a fair rate in the Northern and Central States from about the latter part of March to

NOTABLE *progress, based on scientific research, has been made in controlling that major menace to turkey growing, the blackhead disease. Less attention has been paid to breeding problems. Today the turkey industry would gain by a breeding program based on production records, pedigrees, and progeny testing, like that which has meant so much to progressive breeders of chickens. There is a great need for turkey breeders willing to initiate trap-nesting and pedigreeing, and possessed of the knowledge necessary to isolate superior families and breed from them. State and Federal stations might well lead the way by developing strains notable for certain characteristics of major importance.*

about the first of July. The use of electric lights has helped in getting birds to start laying in January, so that the laying season is extended to approximately 6 months. However, egg production in commercial quantities is still confined to about 6 months of the year, and this means that fresh-killed roasting turkeys must also be a seasonal product unless turkeys can be bred to lay throughout the year. This situation is partially remedied by cold storage, which makes a limited supply of frozen turkeys available at times when there is no fresh stock and

Figure 2.—Trap-nesting—the first step in the pedigree breeding of turkeys.

permits a large turkey crop to be marketed in the fall in an orderly manner without a serious price depression.

The greatest drawback to breeding for high egg production and the other desirable characteristics is the lack of a program based on production records, pedigrees, and progeny testing. Such a program has meant much to progressive breeders of chickens. Here the State and Federal experiment stations can lead the way by developing strains of high-producing turkeys with good viability, quick maturity, and good market quality. The greatest need of the industry today is for a number of breeders who are informed concerning the practices involved in selection and breeding and who are willing to initiate trap-nesting and pedigreeing and, on the basis of the information so obtained, to isolate superior families and breed from them. This is an essential step in the production of a superior strain. Two of the steps involved in the pedigree breeding of turkeys are shown in figures 2 and 3.

THE STATUS OF TURKEY GROWING AS AN INDUSTRY

Turkey raising has been increasing since about 1920 in the United States and now ranks as a 50,000,000-dollar industry. The interest in turkey raising has increased rapidly since that time. It was stimulated by a better knowledge of feeding and more effective control of the disease known as blackhead. The annual loss due to blackhead still amounts to approximately $5,000,000 a year, or 10 percent of the total gross income. In the past, often entire flocks of young turkeys were lost from this disease.

Figure 3.—The final step in the pedigreeing of turkey poults—banding the birds as they are taken from the pedigree baskets.

On January 1, 1920, the census showed 3,627,028 turkeys on 670,834 farms held as breeders after the marketing season. On January 1, 1935, the number had increased to 5,381,912 on 676,114 farms, which is 9.9 percent of all the farms in the United States. The leading States according to the number of turkeys kept were Texas, California, Minnesota, North Dakota, and Oklahoma.

The 1930 census was the first to record the number of turkeys raised rather than the number on farms on January 1. According to this census, there were 16,794,485 turkeys raised in the United States, most of them as a side line to other farm enterprises. The distribution and number of turkeys raised on farms in 1929 is indicated in figure 4. The number of turkeys raised in 1936 has been estimated by the Bureau of Agricultural Economics to exceed 20,000,000—an increase of at least 20 percent over the 1930 figures. There was little increase, however, in the number of farms keeping turkeys. In some localities, turkey raising has reached such proportions as to be a major full-time enterprise, and a great many commercial flocks are large enough to demand the time of one or more persons throughout the year. The largest turkey farm was reported to have produced approximately 50,000 turkeys in 1 year.

New Opportunities Through the Control of Blackhead

From a production standpoint, the opportunities in commercial turkey raising are more promising now than formerly, largely because of improved methods of management that aid in the control of blackhead and other filth-borne diseases.

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Beginning late in the nineteenth century, blackhead invaded one district after another, traveling from east to west with the extension of the turkey industry, until nearly all of the turkey-growing areas became infested with it. It was this disease that ruined turkey growing in the East and Midwest and by 1920 threatened to ruin it everywhere. In the early eighties production per year amounted to

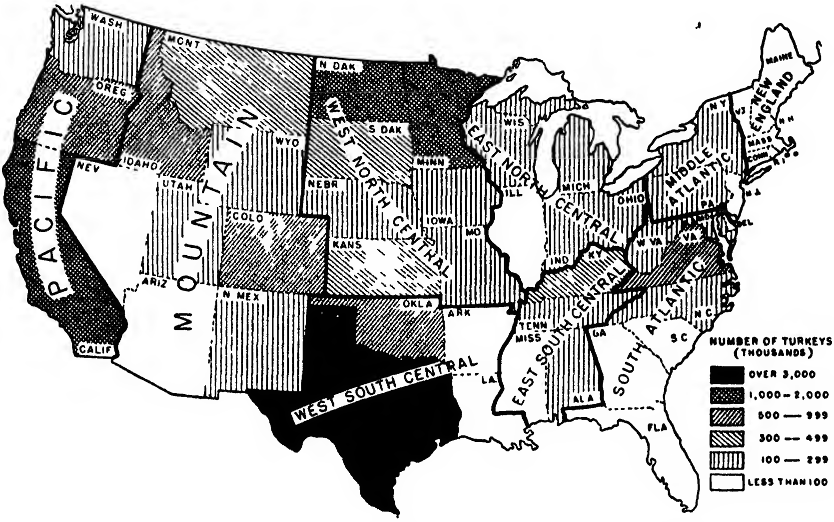

Figure 4.—Number of turkeys raised, by States, in 1929.

one bird for the average American family of about 5 persons, but by 1920 this had been reduced to approximately one bird for 15 persons. Since that time more adequate methods of controlling blackhead have been largely responsible for the increase to approximately one turkey for 6.5 persons. The new knowledge of sanitation and management as it affects the control of blackhead has meant a gradual return of turkey production to the East and Midwest and its firm establishment on a more profitable basis in all sections of the country except the Southeastern States.

MODERN TURKEYS AND THEIR WILD ANCESTORS

Turkeys are now classified by zoologists as a separate family, Meleagrididae, of the order Galliformes, or fowllike birds. In this family there are two genera now living—*Agriocharis*, the ocellated turkey of Yucatan (fig. 5), and *Meleagris*, the North American or common turkey. These genera contain only one species each.

The ocellated or Yucatan turkey (*Agriocharis ocellata*) is confined to the Yucatan Peninsula of Mexico and the adjoining territory, where it dwells in the tropical forests. Its flesh is considered a delicacy. It is smaller than the common turkey, lacks the breast tuft, is brighter colored, has two fleshy appendages on the head instead of one, and has eyed or ocellated tail feathers, from which it takes its name. So far as

is known, it has never been domesticated although natural crossing with the common turkey has been reported. In striking beauty the plumage of the ocellated turkey rivals that of the peacock. The plumage pattern is similar to that of the Bronze turkey although the colors are different. The general effect is green and black with a coppery red iridescence. The large wing feathers of the male are distinctly barred, almost exactly as in the Bronze, while those of the female are indistinctly barred. The head and neck of the ocellated turkey are described as blue, studded with orange warts. The eggs are brown and spotted like those of *Meleagris* but smaller.

Figure 5.—The ocellated turkey (*Agriocharis ocellata*) (male).

Five subspecies (races or varieties) of North American wild turkeys have been described. They interbreed freely with each other and with domesticated turkeys. Table 1 contains a brief description of these subspecies.

TABLE 1.—*Brief description of North American wild turkeys*

Subspecies	Original range	Color description
Meleagris gallopavo gallopavo Linnaeus, the Mexican turkey	Central Mexico	Similar to the Bronze variety but lacks the distinct tail penciling and the heavy-copper colored bronzing. The terminal edgings are almost white
M. gallopavo silvestris Vieillot, the eastern turkey	Eastern United States, excepting southern Florida, to the western and northern limits of the species as described above	Similar to the Bronze but lacks the heavy copper-colored bronzing and the pure white terminal edgings. The latter are dark chestnut or iodine color in *silvestris*
M. gallopavo osceola Scott, the Florida turkey	Florida, at least as far north as Gainesville	Closely resembles *silvestris* but is distinguishable from it by the white bars of the large wing feathers, which, in *osceola*, are much narrower than the black bars and do not cross the shaft of the feather. In all other wild varieties and in the Bronze and Narragansett, the white bars are as wide as or wider than the black ones and extend completely across the feathers
M. gallopavo intermedia Sennett, the Rio Grande turkey	Middle-north Texas to northeastern Coahuila, Nueva Leon, and Tamaulipas	Resembles *silvestris*, but its terminal edgings are light chestnut or cinnamon and its back feathers present a decidedly blackish appearance
M. gallopavo merriami Nelson, Merriam's turkey.	The mountains of southern Colorado, Arizona, New Mexico, western Texas, northern Sonora, and Chihuahua	Resembles *silvestris* but the terminal edgings are creamy to buffy white

The North American wild turkey (*Meleagris gallopavo*, fig. 6) formerly ranged over all of Mexico except the extreme southern and western parts; over southern Ontario, Canada; and over the United States south and east of a line extending from south to north through western Arizona, northeast diagonally across Colorado and Nebraska to include a small portion of southeastern South Dakota, east across

Figure 6.—A flock of wild turkeys at the National Agricultural Research Center. Crosses are being made of the wild on the domestic varieties.

northern Iowa, southern Wisconsin, southern Michigan, northern New York, northern Vermont, northern New Hampshire, and southern Maine.

Wild turkeys, principally the eastern turkey, are now bred to some extent on game farms, both public and private.

Varieties of Domesticated American Turkeys

The turkey, the Muscovy duck, and the Canada (gray) goose constitute the contribution of the Western Hemisphere to the list of species of poultry. At the time North America was discovered, the wild turkey was found in large numbers and, in some instances, had been domesticated by the natives. From the meager historical data available it appears that turkeys were first taken to Spain in 1498. The sources of these and later importations to Europe were turkeys domesticated by the natives of Mexico and Central America. All these turkeys apparently belonged to the Mexican subspecies of the North American turkey. From Spain turkeys were taken to other European countries, being introduced into England between 1524 and 1541. Several European varieties were developed, notably the Cambridgeshire Bronze and the Norfolk Black. From Europe and North America, turkeys were exported to all parts of the civilized

world. They are now raised in Europe, North America, South America, South Africa, Australia, the Philippines, and Hawaii.

After the United States was settled, it appears that the first domesticated turkeys to be raised came not from the native wild stock, but from the domesticated turkeys of Europe. These birds were probably all of the Bronze color pattern, although some Blacks may have been included. For a considerable time no serious attempts were made to domesticate the native wild turkeys, but finally early in the nineteenth century turkey breeders began to cross the domesticated stock with the wild.

About 1830–40, in the Narragansett Bay district of Rhode Island there was developed a local variety which was the forerunner of the modern Narragansett (fig. 7) and Bronze (fig. 8) varieties. About 1860 the first superior strain of Bronze turkeys came into prominence and this variety was described in the first (1871) American Standard of Perfection.

Figure 7.—A Narragansett hen showing typical markings. Wild, Bronze, and ocellated turkeys have the same general pattern although the colors are different.

The development of the Narragansett and White Holland varieties appears to have paralleled approximately that of the Bronze. A color standard for the Narragansett was published in 1874, along with standard descriptions for the Slate, Black, and Buff varieties. The last-named variety never became popular and was dropped from the standard in 1915.

The White Holland was admitted to the standard in 1878 and the Bourbon Red about 1909. Authentic information concerning the origin of the Slate and Buff varieties appears to be lacking. The White Holland variety originated as far as is known in North America, not in the Netherlands, and was developed from white mutations appearing in Bronze flocks. The Black turkey is an old variety that appears to have been developed in Europe, although some strains may have been developed independently in North America. The Bourbon Red had its origin in Bourbon County, Ky., and is the newest of the standard varieties.

According to the American Standard of Perfection all standard-bred turkeys are now classified as one breed, which is subdivided into varieties. The standard varieties all have the same shape and, except for the Bronze, which is a little heavier than the others, they are all

the same size. They are differentiated only by plumage color, and one variety is as good as another for commercial turkey production. However, there is considerable variation within each variety, so that the selection of a good strain is more important, from the standpoint of economical production, than the selection of a variety. Six stand-

Figure 8.—A farm breeding unit of Bronze turkeys.

ard varieties of domesticated turkeys are now bred in the United States. The data in tables 2 and 3 show some of the characteristics of these varieties.

TABLE 2.—*Standard weights of the six standard varieties of American turkeys*[1]

Variety	Adult tom	Yearling tom	Young tom	Yearling and adult hen	Young hen
	Pounds	*Pounds*	*Pounds*	*Pounds*	*Pounds*
Bronze	36	33	25	20	16
White Holland, Narragansett, Bourbon Red, Black, and Slate	33	30	23	18	14

[1] The weights shown are for young turkeys 8 to 12 months of age, for yearlings 12 to 24 months of age, and for adults 24 months of age or older. Actually, very few flocks of turkeys attain standard weights.

TABLE 3.—*Color of the six standard varieties of American turkeys*

Variety	Plumage color	Shank color
Bronze	Ground color is dull black but the exposed surfaces of the feathers are glossed with rich iridescent red green on the fore part of the body and with a brilliant copper-colored bronzing edged with black on the rear half. On the tail, tail coverts, and sides there is, in addition, a terminal edging of white, which also appears on the breast feathers of the female. Main tail feathers and tail coverts are distinctly penciled, medium brown and black.	Blackish in young birds, pinkish in adults.
Narragansett	The plumage pattern resembles that of the Bronze, but there is no red-green sheen and no bronzing. The Narragansett colors are metallic black with light steel-gray edging bordered in certain sections by a narrow black band on the ends of the feathers; main tail feathers and tail coverts distinctly penciled, light brown and black.	Blackish salmon in young birds; deep salmon in adults.
White Holland	White in all sections	Pinkish white.
Bourbon Red	Dark brownish red with white wings. The breast feathers have narrow black tips which,in the females, are bordered with white. The tail is white with an indistinct reddish bar near the end.	Reddish brown in young birds; reddish pink in adults.
Black	Black in all sections	Slate black in young birds; pink in adults.
Slate	Slate color in all sections	Pink

Past Work in Breeding

Even when raised in captivity and given every opportunity to make maximum growth, wild turkeys are smaller than their domesticated relatives. According to reliable observations, young North American wild turkey toms, when in good condition, in December and January average approximately 12 pounds in live weight and the young hens about 8 pounds. The adult wild males usually weigh from 19 to 22 pounds and in rare instances attain a weight of 33 pounds when fat. When grown in captivity under favorable conditions, the live weights of wild turkeys are somewhat greater than those mentioned. However, there is a decided contrast between the weights commonly attained by strains of Bronze turkeys and the much smaller weights attained by wild turkeys even when they are raised under similar conditions. Egg production in the better strains of modern turkeys has been increased substantially over that of the wild turkey. Progress in breeding for plumage color is evident by the variety of colors and patterns in the domestic birds. Some improvement in type has also been effected. The wild turkey has a rather shallow body, a long neck, a slender head, and long legs. The breeders of domesticated turkeys have developed a larger bird with a deeper body, shorter legs and neck, and heavier fleshing except over the breast, where the wild turkey is probably the equal of the domesticated bird.

Improvements made have been few and slow and thus the good qualities of the original stock have not been sacrificed. For example, the eggs laid by domesticated turkeys are as fertile and hatch fully as well as those laid by wild turkeys, and modern strains of turkeys are as resistant to disease as the wild type. Rate of maturity to market condition has been little influenced by domestication.

Comparatively little inbreeding or cross-breeding has been practiced in turkey breeding, except by a very few breeders who have developed distinctive strains or new varieties.

Private breeders have been responsible for the development of the modern turkey in all its beauty and usefulness. However, there is no accurate, detailed history of breed development and there has never been a pedigree-recording system for turkeys similar to the herdbook used with other animals. Such evidence as there is has been summed up in the preceding paragraphs.

Today the Bronze variety predominates to an overwhelming extent. Narragansetts, White Hollands, and Bourbon Reds are fairly common and appear to be gaining in popularity. The Black variety is less common although it too is probably gaining in favor. The Slate turkey may be classified as rare and the wild turkey as rare except on game farms.

MARKET TRENDS AND THEIR RELATION TO BREEDING

So far turkeys have been produced almost exclusively for roasting purposes and marketed between 6 and 8 months of age. Turkey broilers or fryers have not been produced in significant numbers and there is little reason to believe that they will ever be a factor in the turkey industry since smaller types of poultry fulfill this need. Turkey capons have been successfully produced but have not met with

special favor on the markets. Until they do, the extra cost of production will not be justified. Turkey eggs, although palatable and suitable for cooking, do not possess the delicacy of flavor and fineness of texture characteristic of chicken eggs. The profitable production

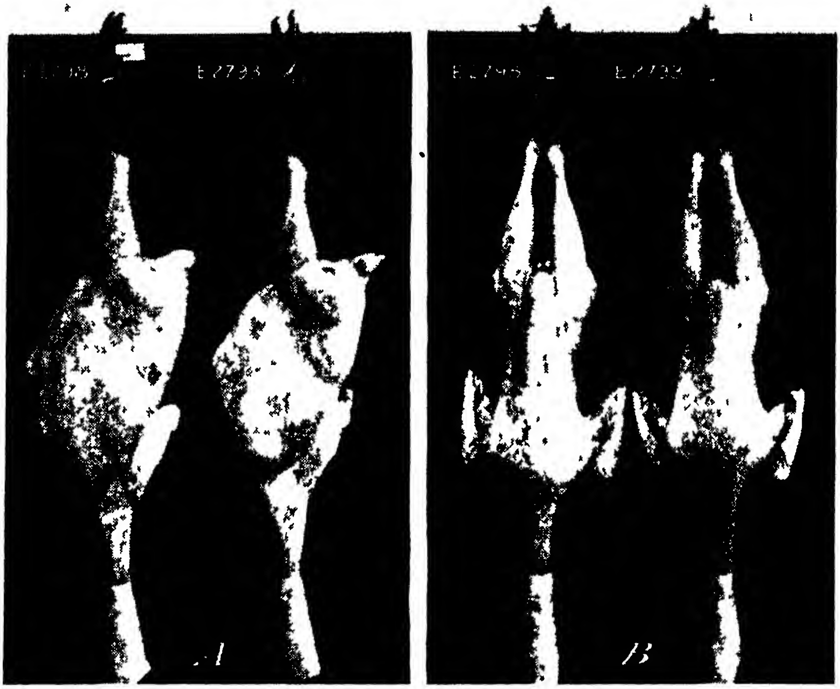

Figure 9.—Illustrating body type in dressed turkeys. *A*, Two young Black toms No. 2798, on the left, when killed at the age of 32 weeks, weighed 22.6 pounds (dressed), had a narrow poorly meated breast, a keel measuring 8.2 inches long and a shank 8.1 inches long and produced 3.9 pounds of breast meat. No. 2793, on its right weighed 22.3 pounds, had a broad well-meated breast, a keel bone measuring 7.5 inches in length, and a shank 8.3 inches long, and produced 4.1 pounds of breast meat. It is desirable to have a broad well-fleshed breast. The keel should be as long as the shank or longer. (Length of shank is distance between rear of hock joint and the ball of the foot.) *B*, Side view, no. 2798 on left, no. 2793 on right.

of market eggs from turkeys seems highly improbable even as a sideline enterprise for the turkey grower.

According to various observers, most but not all larger eating establishments and individuals buying for large dinner groups prefer turkeys weighing more than 15 pounds (dressed) while most of the smaller places and American housewives in general prefer dressed birds weighing less than 15 pounds. This preference for small turkeys by what is now the majority of consumers has increased the demand for hens and small toms.

Accurate estimates of the average weights at which turkeys are marketed throughout the country are not available, but the average

for young hens probably ranges, in different producing areas, between 9 to 12½ pounds live weight and 8 to 11½ pounds dressed weight (blood and feathers removed). The average for young toms probably ranges between 15 to 21½ pounds live weight and 13½ to 19½ pounds dressed weight. In some producing areas where large stock and good feeding methods are used, the average body weight will be larger than in other sections. A few years ago the average body weight of turkeys was smaller than at the present time, but the advent of commercial turkey raising with better feeding methods and stock bred for large size has increased the average weights. Standardbred young Bronze tom turkeys raised on full feed will average 18 to 19½ pounds dressed, and young hens 10½ to 11½ pounds, when marketed at the age of 26 to 28 weeks. Birds from strains of extra large turkeys may exceed these weights by 25 percent or more. Figure 9 *A* and *B* illustrates body types in dressed turkeys.

The present demand for smaller turkeys appears to be based on sound economics—the fitting of the dressed turkey unit to the needs of two great groups of consumers, the small-scale vendor of cooked turkey meat and the average family. For large family groups and for hotels and restaurants, the large turkey is in demand, as large toms dress out better than small toms and are fully as palatable. At the present time, the market receipts of large turkeys are slightly in excess of the demand, resulting in a price differential of ½ to 4 cents per pound in favor of hen turkeys and small toms. Unless the demand changes, which appears unlikely, future breeding operations in turkey production should be in the direction of smaller turkeys.

RESEARCH IN TURKEY BREEDING

There has been little breeding research with turkeys. One drawback has been the lack of sufficient funds for this purpose; a lack of adequately trained personnel with the proper interest in this aspect of poultry production; and third, the susceptibility of turkeys to blackhead—but this last drawback is being rapidly overcome.

A brief description of the results of scientific investigations to date follows and a list of references is included at the end of this article.

Work of State Experiment Stations

Except for matings to replenish flocks, turkey-breeding work has not been carried on extensively by the State experiment stations, though a few have initiated projects in the past or have some work under way at the present time.

Studies on the inheritance of plumage color have been limited and only a few individuals were used in the experiments from which conclusions were drawn. Some of the more important findings may be summed up as follows: (1) Black plumage color is imperfectly dominant to the bronze plumage pattern and imperfectly epistatic [1] to the Narragansett plumage patterns and red plumage color. (2) Red plumage color and Narragansett plumage pattern are epistatic to the bronze plumage pattern. (3) The factor for slate plumage color is a dominant dilution factor affecting the bronze and black

[1] Characterized by the dominant action of a gene over another gene situated on a different chromosome or at a different place on the same chromosome.

plumage patterns to produce slate-colored turkeys, or red plumage to produce slate-red turkeys. (4) The factor providing for the presence of plumage color is dominant to the absence of pigmentation of plumage. When allowed to express itself, the recessive factor produces a white bird that has brown eyes because this particular factor affects plumage color only and does not affect eye color. All white birds, therefore, carry the plumage pattern or color for bronze, Narragansett, black, or red but do not show any of these patterns or colors unless they are crossed with colored turkeys. However, when mated together, these white turkeys always produce white offspring. (5) Buff-colored turkeys may be produced by first crossing black turkeys with red ones. The resulting rusty black offspring are then crossed back to the red turkeys, which results in progeny having four types of plumage color—rusty black, Bourbon Red, bronze red, and buff. (6) The factor for Narragansett plumage color pattern is recessive and sex-linked. Males showing the Narragansett plumage pattern are produced only from matings of Narragansetts, but females showing Narragansett color and males showing bronze color may be produced from a mating of Narragansett males and bronze females. The reciprocal of the mating produces all bronze-colored progeny.

Work of the Federal Government

In the field of plant and animal genetics, there has been a good deal of experimental work in making wide crosses such as crosses between species. Certain of these results have been worth while. This is more true of plants than of animals, although the mule is an outstanding example of a useful wide cross in the animal kingdom. In most cases, however, the hybrid proves to be without economic value, although this means of obtaining a cross of unusual value cannot be overlooked.

An attempt was made by Quinn, Burrows, and Byerly at the National Agricultural Research Center, Beltsville, Md., to effect an intergeneric cross between the turkey and the chicken by the use of an artificial insemination technique developed at the center. Semen of turkey males was used to fertilize Rhode Island Red females and semen from purebred and cross-bred chicken males was used to fertilize turkey females. About 20 percent of the eggs laid by the turkey females were fertile, but all except one died in the early stages of embryonic development. In the reciprocal cross only a few of the eggs were fertile and all of these died within a 3-day period of incubation.

Although 25 percent of the fertile eggs died as embryos during the first day of incubation, one hybrid embryo, from the chicken male × turkey female cross, lived until it was fully developed and apparently ready to hatch. This hybrid embryo was found dead in the shell on the twenty-eighth day of incubation, death having occurred some time between the twenty-third and twenty-eighth days. No daily observations were made after the twenty-third day, so that the exact time of death, and the age of the embryo when death occurred, were unknown. The hybrid was obtained from an agg laid by a Bronze turkey hen on July 3, 20 days after the last fertile turkey egg had been obtained and 66 days after the removal of the turkey male.

The turkey-chicken hybrid was intermediate in conformation between the chicken and the turkey. The hybrid was also lighter in down color than the turkey, having a reddish cast in both head and body. It had yellow shanks whereas the shanks of the turkey parent were quite dusky. The hybrid had a distinct comb and no evidence of the characteristic fleshy protuberance of the turkey. It also showed a polydactylism in which the fourth toe of the left foot was triplicated, a malformation sometimes found in wide crosses. In various external characteristics such as head type and shape, down color and shank color, the turkey-chicken hybrid may be said to have shown the characteristics of the chicken rather than the turkey.

The latest development in poultry breeding for the creation of superior strains is the building up of inbred strains in order to produce successful hybrids by subsequent crossing. It is much more difficult to build up inbred lines of chickens or turkeys than of many plants, since fewer individuals can be used and self-fertilization cannot be practiced.

Although he cannot catalog the characteristics of the turkey, and their mode of inheritance, the scientific breeder might accumulate and purify certain good characteristics by the process of inbreeding, which fixes various good and bad traits of the parents in the different lines of inbred progeny. Sires that show an accumulation of bad traits might be discarded. A line that showed an accumulation of good traits might be crossed with another good line, with the object of producing superior hybrid individuals.

Because inbreeding might play an important role in the improvement of turkeys in some such way as this, an experimental turkey-breeding project was begun in 1931 by the Bureau of Animal Industry at its range livestock experiment station, Miles City, Mont. This project was terminated in 1935 and the results of approximately 5 years' work were summarized. One purpose of the project was to measure the effect of inbreeding on the fertility and hatchability of eggs, the egg weight, and the egg production of Bronze turkeys. In order to make an adequate comparison of the effects of inbreeding, a series of outbred matings were maintained. These outbred matings were made between unrelated or distantly related individuals, and each year the progeny was systematically outbred with the idea of maintaining a line indefinitely without resorting to close inbreeding or the introduction of new stock. This plan of outbreeding included seven matings and constituted a separate experiment that will be discussed later.

TABLE 4.—*Summary of the egg fertility and hatchability and of egg production and egg weight for 773 inbred and outbred Bronze turkeys*

Degree of inbreeding	Coefficient of inbreeding	Fertility	Hatch-ability	Production of eggs to June 1	Average egg weight
		Percent	*Percent*	*Number*	*Grams*
Outbred	0.000–0.063	87.8	67.6	47.7	83.6
Mild	.125– .218	75.4	51.7	42.2	82.7
Close	.250– .411	82.8	52.8	39.0	82.1
Intensive	.500– .672	69.3	34.9	41.4	81.5

The data in table 4 show the results obtained from unrelated turkey matings and from matings of different degrees of relationship on fertility, hatchability of eggs, egg weight, and egg production.

Some general conclusions from this work are as follows:

(1) Mild and close inbreeding had little effect on fertility, egg production, and egg weight when compared to outbreeding.

(2) Mild and close inbreeding had an adverse effect on the hatchability of turkey eggs. The inbred lines averaged approximately 52 percent hatchability whereas the outbred lines averaged 67.6 percent.

(3) Intensive inbreeding adversely affected fertility and hatchability of eggs but had slight effect on production and average egg weight.

These conclusions are taken from the final averages. However, there was considerable variation in the results obtained from various matings within each of the four groups. For instance, some of the mild and close inbred turkeys gave better results in regard to the four factors considered than the outbred turkeys that were used as controls. In other words, it appears that it might be possible with careful selection and mating to obtain lines of inbred turkeys that would be as good as the outbred turkeys in these respects.

Matings were made between unrelated or distantly related individuals each year and systematically outbred with the idea of establishing a line of outbred turkeys without resorting to close inbreeding or introduction of new stock. The method used was briefly as follows:

The start was made with stock purchased from seven different breeders. Seven breeding pens were mated in such a way that the males and females in no two pens were from the same source. The progeny were individually wing-banded, which made it possible to identify the progeny of each mating at any time. The best young hens and the best young tom turkeys were selected in each generation in each pen. The selected young hens from each pen remained together as a breeding unit each year and were placed in the pen previously occupied by their parents, but the selected young tom was placed in the next pen. For example, the selected young hens from the mating in pen 1 were placed in pen 1 the next year. The best young tom available from this mating, however, was placed in pen 2. The young tom turkey from pen 2 was placed in pen 3, and so on, the young tom from pen 6 being placed in pen 7, and that from pen 7 being placed in pen 1. This revolving process was followed each year.

The plan proved to be satisfactory, simple, easily workable, and effective in maintaining the average egg weight and improving the fertility and hatchability of eggs and egg production. The data in table 5 show the results obtained in the operation of this plan for 5 years. It is regrettable that it was necessary to sell the progeny of the 1935 matings before records of egg production and egg weight could be obtained.

Practical breeding operations are well served by basic research, especially in a field so new as turkey breeding. The mode of inheritance of characters, the physiology of reproduction, and the study of mating systems all have a direct application to practical problems. Through these findings, unwise practices may be brought to light and discarded and more efficient methods developed.

TABLE 5.—*Summary of the egg fertility and hatchability and of egg production and egg weight for 390 systematically outbred turkeys*

Year	Coefficient of inbreeding	Fertility	Hatchability	Production of eggs to June 1	Average egg weight
		Percent	*Percent*	*Number*	*Grams*
1931	0.000	72.7	55.2	44.6	84.7
1932	.000	85.0	56.6	47.4	85.0
1933	.031	92.0	71.4	49.6	79.6
1934	.060	85.3	68.7	48.6	84.0
1935	.053	92.6	74.9		

SELECTED LIST OF REFERENCES

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Some workers identified with turkey-breeding work at State and Federal experiment stations

State	*Worker*	*Location*
California	L. W. Taylor,[1] V. S. Asmundson	Davis.
Indiana	C. W. Carrick,[1] E. E. Schnetzler	LaFayette.
Iowa	H. L. Wilcke [1]	Ames.
	W. R. B. Robertson	Iowa City.
Kansas	L. F. Payne,[1] H. M. Scott, D. C. Warren.	Manhattan.
Kentucky	J. H. Martin,[1] W. M. Insko, Jr	Lexington.
Michigan	C. G. Card,[1] F. N. Barrett	East Lansing.
Nebraska	F. E. Musschl,[1] H. E. Alder	Lincoln.
New Mexico	L. N. Berry [1]	State College.
North Dakota	F. E. Moore,[1] O. A. Barton	Fargo.
Oklahoma	R. B. Thompson,[1] Robert Penquite, O. E. Goff.	Stillwater.
Pennsylvania	H. C. Knandel,[1] D. R. Marble, P. H. Margolf.	State College.
Utah	Byron Alder [1]	Logan.
Wisconsin	J. G. Halpin,[1] G. E. Annin	Madison.
Wyoming	F. S. Hultz,[1] M. O. North	Laramie.
U. S. Department of Agriculture, Bureau of Animal Industry.	Berley Winton,[1] S. J. Marsden, C. W. Knox, J. P. Quinn, W. H. Burrows.	Washington, D. C.

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DUCK BREEDING

A. R. LEE, Associate Poultry Husbandman, Animal Husbandry Division, Bureau of Animal Industry

RELATIVELY little information is available on the breeding of ducks and practically no genetic investigations have been made on the improvement of the breeds. Because of the lack of records, no survey of duck breeding has been made, nor has the Department of Agriculture used ducks in its breeding investigations. The same is true of practically all the State experiment stations. On the other hand, although Federal research in poultry breeding has not dealt specifically with ducks, it has dealt with fundamentals in genetics, and principles of management have been worked out that are applicable to all poultry, including ducks. The size and extent of the duck industry in this country seem to warrant careful study of this important aspect of poultry breeding.

Duck raising is conducted as a side line in nearly all sections of the United States, where ducks are kept in small flocks on general farms. These farm flocks are kept primarily for meat production and while the birds have been selected for size and market type, very little attention has been given to careful pedigree breeding. Commercial duck raising has been extensively developed as a highly specialized industry on Long Island, N. Y. (fig. 1) and to some extent on a few commercial duck farms in several other sections of the country. Relatively little has been published on the methods used in the selection and breeding of ducks on these commercial duck farms.

Few ducks have been bred for high egg production in this country because of the lack of demand for duck eggs as food. Relatively few ducks of the breeds especially adapted for egg production have been kept here and few ducks with high egg records have been produced. That ducks can be bred for very high production has been demonstrated in many egg-laying contests in other countries, in which the duck records have equaled or exceeded the best records made by chickens either here or abroad.

PRODUCTION OF GREEN DUCKS

ALTHOUGH most flocks of ducks are small, about 12 million ducks are raised each year in the United States. They are raised in every State, the greatest total farm production occurring in the North Central States. Large commercial duck farms in New York place that State first in total number of ducks raised, Long Island alone producing nearly a million annually. These market ducks from the large commercial flocks are called green ducks. They are hatched in the winter and early in the spring, forced for rapid growth, and marketed

at 9 to 13 weeks of age when they attain a weight of 4½ to 6 pounds each. Ducks produced on general farms are not forced for rapid growth; they are hatched in the spring and marketed in the fall and winter when they are 5 to 7 months old. These ducks from farm flocks, although twice as old when they are marketed, are little if any larger than the green ducks.

The number of ducks raised in this country is about three times the number of geese but less than two-thirds the number of turkeys.

Figure 1.—The Pekin duck is the only breed used for commercial duck farming. A large number of duck farms have been developed along the inlets of Long Island.

Duck production is similar to turkey production in that both ducks and turkeys are raised primarily for market as young birds, and relatively few breeders or mature birds are kept. While chicken and turkey production have shown a marked increase during the last 25 years, duck production is barely holding its own. Ducks are primarily in demand in the large cities, especially among persons of foreign extraction. The number of ducks kept in proportion to the total population is much lower in the United States than in most other countries, where there is a better demand for duck meat and for duck eggs.

ORIGIN AND HISTORY OF DOMESTIC DUCKS

All domesticated ducks, with the exception of the Muscovy, are descended from the wild mallard (fig. 2). While actual references to ducks go back to only a few years previous to the Christian era, it is reasonable to suppose that wild mallards were domesticated at a much earlier period than this. Common domestic ducks of Europe, among which there was a variety of colors, were brought to the United States by the early settlers.

There are three classes of ducks—the meat class, the egg class, and the ornamental class. Only a few representative breeds of each class

will be discussed in this article. In the meat class, the Rouen, Aylesbury, Pekin, Cayuga, and Muscovy are among the well-known breeds.

The Rouen, which has the same color markings as the wild mallard, shows the effect of domestication by its greatly increased size and superior fleshing qualities. This breed originated near Rouen, France, whence it derives its name, but it was greatly improved in England, where it was bred for very large size, the males weighing 9 to 11 pounds alive and the females 8 to 10 pounds. It was brought

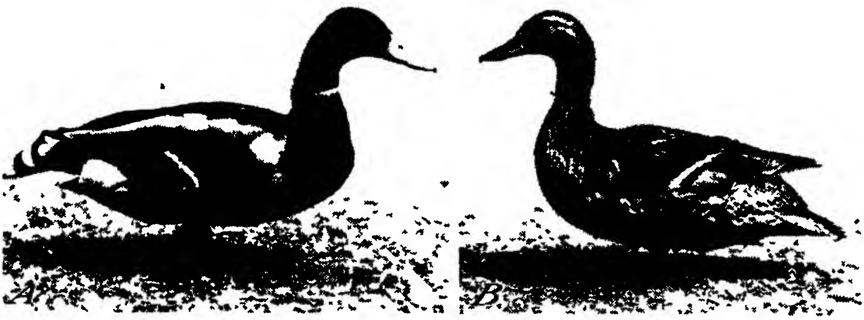

Figure 2.—Wild mallard, drake (*A*) and duck (*B*)—the ancestors of all but one of our domestic breeds of ducks.

into the United States about 1850 and became quite popular but is now kept in this country primarily by fanciers.

The Aylesbury is a white duck that originated in England early in the nineteenth century. It is a large duck with a massive body, that is carried nearly horizontal. The Aylesbury duck was first brought into this country about 1849 and was used on the first duck farms, but was eventually replaced by the Pekin. Duck breeders in this country consider it less hardy than the Pekin.

The Pekin duck (fig. 3) originated in China and little is known of its history in that country. It is a white duck of medium size, more upstanding in type than the Aylesbury, an excellent market bird and noted for its vigor and hardiness. The breed was brought into the United States from China in 1873. It rapidly became popular and soon replaced all other breeds for commercial duck raising. Crosses were made of the Pekin with Aylesbury and other breeds, but the pure Pekin was found to be much better adapted for commercial duck farming and has since maintained this position as the best and only commercial market duck. The first small importations of Pekins, from which most of the present commercial flocks are descended, were very good market ducks, not greatly different in appearance, size, or other economic characters from those of today.

The Cayuga duck (fig. 4, *D*) is of interest because it was produced in Cayuga County, N. Y., and also because it is solid black in color. It was developed about 1850 and was just becoming well known when the Pekin, which was better adapted for the market, came along and replaced it.

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The Muscovy, or Brazilian, duck is a native of Brazil and is considered a different species from the wild mallard and from the other domestic ducks. The period of incubation for Muscovy eggs is 33 to 35 days, compared with 28 days for eggs of other domestic breeds of ducks. The breed was introduced into the United States between 1840 and 1850. The Muscovy drake is about one-third larger than the duck, while in all the other market breeds the male and the female are practically equal in size.

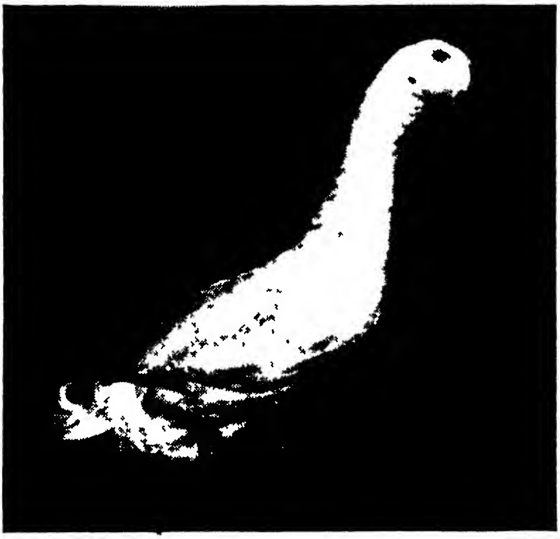

Figure 3.—Most of the commercial flocks of ducks in this country came from two small importations of Pekin ducks brought from China in 1873.

The egg-laying class, of which the Indian Runner (fig. 4, *E*) is the outstanding breed in this country, was brought into United States only about 40 years ago. It is an upright Penguin type of duck noted for great prolificacy. It was named Indian Runner because of its supposed introduction from East India, but the evidence appears to show that it was a selected duck of a type common in Belgium and the Netherlands. Because of its small size it is not so well adapted as the Pekin for meat production. The Khaki-Campbell duck is a popular breed of this class in foreign countries.

In the ornamental class there are ducks of all sizes, types, and colors, which indicates that great variation has been brought about through selection and breeding. The Call (Fig. 4, *A* and *B*) and the Black East India are bred for extremely small size, the White and Gray Calls being miniatures of the Pekin and Rouen, respectively, while the East India is a small-sized Cayuga. The Mandarin and the Wood ducks are the most ornamental of the small breeds of waterfowl. Their plumage contains many brilliant colors and is handsomely marked. In the ornamental class there are also larger ducks, such as the Crested White (Fig. 4, *C*), which is distinguished by a well-developed crest on the top of its head. Figure 4 shows a few of the variations that occur in the breeds of ducks.

Improvement by Breeding

Improvement of ducks of the meat class in this country has been largely confined to the selection of a few individuals notable for size, type, and rapid growth out of the large number raised for market each year. On commercial duck farms 40 or more young ducks are

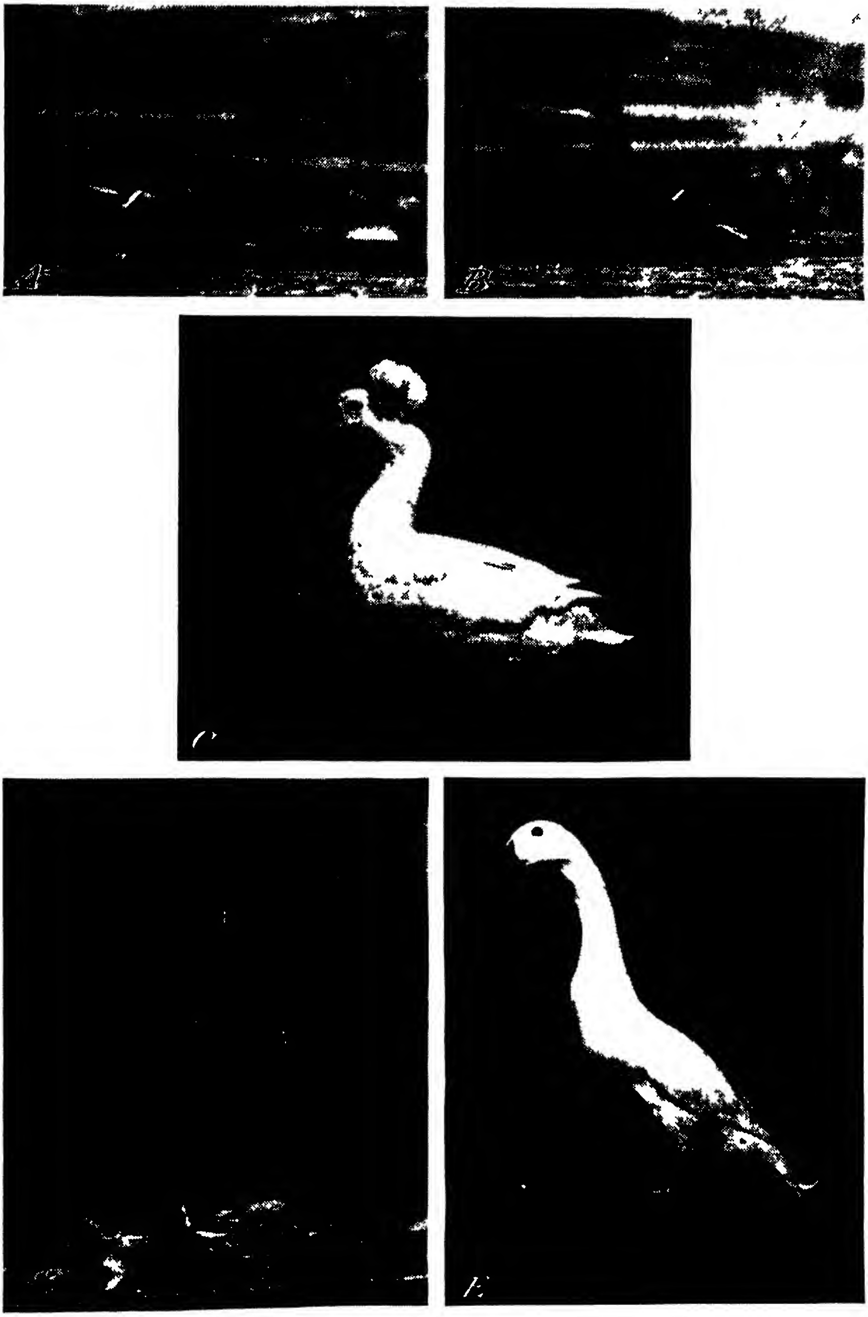

Figure 4.—Great variation has been produced in ducks through selection and breeding: *A*, Gray Call male; *B*, Gray Call female; *C*, Crested White; *D*, Cayuga; *E*, Indian Runner.

marketed annually from each female breeder. Selection of a few of the outstanding birds from a large flock does not give an accurate measure of the breeding value of the flock, but this selection, starting from high-quality stock, has resulted in the production of very uniform flocks of Pekin ducks. These ducks are noted for their rapid growth and for uniformity in size and type. Pekin ducks have not been bred or selected for high yearly egg production but they lay very steadily during the months when eggs are desired for hatching.

Principles of Breeding

An article by Jull in the 1936 Yearbook of Agriculture[1] contains a thorough discussion of the principles of breeding, the use of inbreeding and cross-breeding, breeding for disease resistance, and other aspects of poultry breeding that apply to ducks no less than to chickens. A careful study of the breeding investigations that have been made with chickens and with turkeys should be of much assistance to those interested in improving the breeding of ducks. No attempt will be made to discuss these breeding principles in detail here—for this information the reader is referred to Dr. Jull's article.

Jull stresses the importance of what he calls a three-p program, involving production records, pedigrees, and progeny testing. Production records, he points out, are of great value; yet many good individual producers fail to produce good offspring. Pedigree breeding, in which detailed records are kept of the breeding birds and their offspring, is an improvement over breeding from production records alone, but again there is no positive assurance that a bird with a good ancestry will always produce good offspring. Since ducks are rarely trap-nested, practically no thorough pedigree breeding has been carried on with them. Progeny testing, which is the best method of evaluating any poultry breeding stock, has not as yet been applied to the breeding of ducks in this country.

In fact, ducks offer a virgin field for poultry breeding research, especially in the inheritance of meat characters. The first practical steps in a breeding program would be the use of the production record, the pedigree, and the progeny test. They involve expense, however, in the keeping of records, securing individual egg records, and maintaining breeding ducks beyond the age now customary; and duck breeders apparently do not feel that this expense is justified under present conditions. A very different situation exists among breeders of chickens, who are primarily interested in breeding for eggs.

Breeding for Size and for Quality of Flesh

Ducks are kept and selected primarily for flesh production. Good body type and rapid growth to market size are desired for economical production. But very little research work has been done on the breeding of poultry for meat or flesh production or on the inheritance of body size. W. F. Waters of the Iowa Agricultural Experiment Station has shown that inheritance of body size in chickens is extremely complex, and experiments in crossing a large and a small breed at the National Agricultural Research Center, Beltsville, Md., indicate that a large number of genes are involved.

[1] See list of selected references, p 1377

As already indicated, breeding work with Pekin ducks has been confined principally to the selection of birds of the desired market type, size, and weight, that is, those weighing about 5½ pounds when dressed at 10 to 12 weeks of age. A larger Pekin can easily be produced, but it would not be so well adapted to the market demand; moreover, large heavy ducks are not usually as good breeders as those of medium size. Since only a small percentage of the ducks raised are kept for breeding, it is a relatively easy matter to select good-sized, rapid-growing, and early-maturing birds for the breeding flocks.

Inbreeding and Hatchability

The Pekin ducks have been bred for a longer period without introducing outside stock than have any of the popular breeds of chickens. No work on the use or effect of inbreeding in the egg-laying breeds of ducks has been reported. The results secured with inbreeding chickens for egg production should be applicable to the breeding of ducks. Almost all the Pekin ducks in this country are descended from two small importations. There have been periods when it would appear that many of the flocks on Long Island were being too closely inbred and that this resulted in widespread poor hatchability. From experiments with chickens it has been concluded that hatchability tends to decrease and chick mortality tends to increase with close inbreeding.

Hatchability is an inherited character that can be improved by careful selection and breeding. However, the fact that Pekin ducks are usually mass mated and are rarely trap-nested makes it very difficult to select for hatchability. In these mass matings there is usually one male for every six or seven females. It would be very desirable to select males for breeding on the basis of high hatchability of the eggs of their dam and their progeny.

Cross-Breeding

It is sometimes claimed that cross-breeding produces increased vigor in the offspring. There has been very little cross-breeding of ducks except in farm flocks where the birds are bred indiscriminately. The purebred Pekin is the only breed used on commercial duck farms in this country for meat production. Ducks of the Aylesbury breed were occasionally crossed with the Pekins in this country some years ago, but the reports of this introduction of Aylesbury blood have been unfavorable and these crosses have been entirely eliminated from the breeding flocks. It is reported that outcrosses of the Pekin on the Aylesbury are occasionally made in England to improve the breeding qualities of certain flocks that show poor fertility and lack of vigor. The mule duck, a cross of the Muscovy on the common domestic duck, is occasionally made, especially in the Southern States. The hybrids are not fertile when bred together, but they will breed to some extent with either parent race.

Selection for Disease Resistance

Ducks are considered less subject to disease than chickens, and mortality in commercial flocks, both in the young ducks and in the mature stock, is usually much less than with chickens. Commercial

duck breeders started with good Pekin stock and appear to have kept their ducks relatively free from disease by good management of the breeding flocks. No experimental work has been reported, however, on breeding ducks for disease resistance. There has doubtless been much less chance for the spread of disease than in the case of chickens, since most ducks are very healthy, and commercial duck farming is a highly specialized industry largely conducted on very light sandy soil by a small number of breeders who usually hatch and raise their own

Figure 5.—**Pekin ducks, 12 weeks of age, weighing 6 pounds each, and ready for market.**

stock, while the ducks on general farms are kept in very small flocks and hatched and reared by natural methods with very little trade in day-old ducklings or breeding stock.

Breeding for Meat Production

On commercial duck farms picking out breeders has been almost entirely a matter of selection from appearance and by handling the birds. Ducks have been bred from large flock matings; few if any special matings have been made; the birds are not trap-nested and there has been no selection of outstanding breeders on the basis of individual pedigree records. However, the uniformity of the original stock and the selection of small flocks of breeders from very large numbers of ducks have brought about a much greater uniformity in type and size than can be found in any other kind of poultry (fig. 5). The best flocks of ducks are so highly bred that there is practically only one market grade.

The best-appearing young birds are selected when they are 8 to 10 weeks old and reserved for further selection as breeders. At this age the birds intended for market are changed to fattening rations.

Breeding males are usually selected during June and females during the early part of July. When these selected ducks reach market age they are again carefully examined and only the best are kept. Breeding ducks are selected for good length, width, and depth of body, and for early maturity. While good size and quick growth are desired, stock showing any sign of coarseness is discarded. Heavy birds with very deep keels have a tendency to take on too much fat and are likely to show low egg production, poor fertility, and lack of vigor. Most breeding ducks are kept only through their first laying season, as young ducks are better producers and lay earlier than older ones. The use of only mass matings and this restriction to young breeding stock made it impossible to do any careful pedigree breeding or progeny testing. Retaining a few of the best breeders for a second season and keeping adequate records for these birds would be worth trying.

Young Pekin ducks are efficient producers of meat. The young ducks raised on commercial farms have been selected and bred for rapid growth and at 10 to 12 weeks of age they are nearly as large as they are at maturity. At 12 weeks of age Pekin ducks weigh about 6 pounds, or 50 times their initial weight. Chickens fed for rapid growth and marketed as broilers at 12 weeks of age weigh about 2½ pounds, or less than one-half as much as ducks of the same age, while at maturity the ducks weigh about the same as chickens.

Up to about 1910 market growers exhibited their ducks at the poultry shows and competed to some extent in the sale of breeding stock meeting standard requirements. Since that time commercial duck farmers have shown much less interest in the requirements of the standard, largely disregarding any points that did not meet their own particular market demands.[2]

Breeding for Egg Production

Ducks of the egg-laying class have been selected and bred for very high egg production. Records of individual ducks and of small flocks show egg yields as high in number as the best records made by hens, and higher in total weight. In this country there is very little interest in the egg-producing breeds of ducks, largely because of lack of demand for duck eggs for market. The Indian Runner duck, which is one of the best egg producers, experienced a moderate boom beginning about 1907, but the interest in the breed lasted only for about 7 or 8 years.[3] Duck eggs are usually in good demand only early in the spring, especially around Easter time. There has been some indication of a slightly increased demand during the last year or two in some markets.

Duck egg-laying contests have been conducted in England and other foreign countries, where the egg breeds are kept much more extensively than they are in the United States. Trap nests used in Germany are

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[2] The first standard for Pekin ducks was published in 1874 and the following year this breed was admitted to the standard of the American Poultry Association. In 1888 the following standard weights were adopted: Old drake, 8 pounds; old duck, 7 pounds; young drake, 7 pounds; young duck, 6 pounds. In 1910 the weights were increased 1 pound in each class and more emphasis was placed on development of ducks with deep bodies and long keel bones.

[3] The Indian Runner duck standard was first adopted by the American Poultry Association in 1898. Relatively few changes have been made in the standard and these changes have been largely confined to minor points. Standard weights are 4½ pounds and 4 pounds for adult drakes and ducks, respectively The standard calls for a long slender bird with carriage approaching the perpendicular. The so-called utility type of Indian Runner duck, bred only for egg production, is less upright in carriage and not so slender as the standard type, which is bred primarily for exhibition.

illustrated in figure 6. The 161 ducks entered in one of the English contests averaged 225 eggs in 48 weeks. The average weight of all eggs was 2.57 ounces, which gives an egg production per duck of 36 pounds, 3 ounces, or about eight times the average weight of the ducks of the egg-laying class. This is a much greater average production per pound of body weight than is made by chickens in the egg-laying

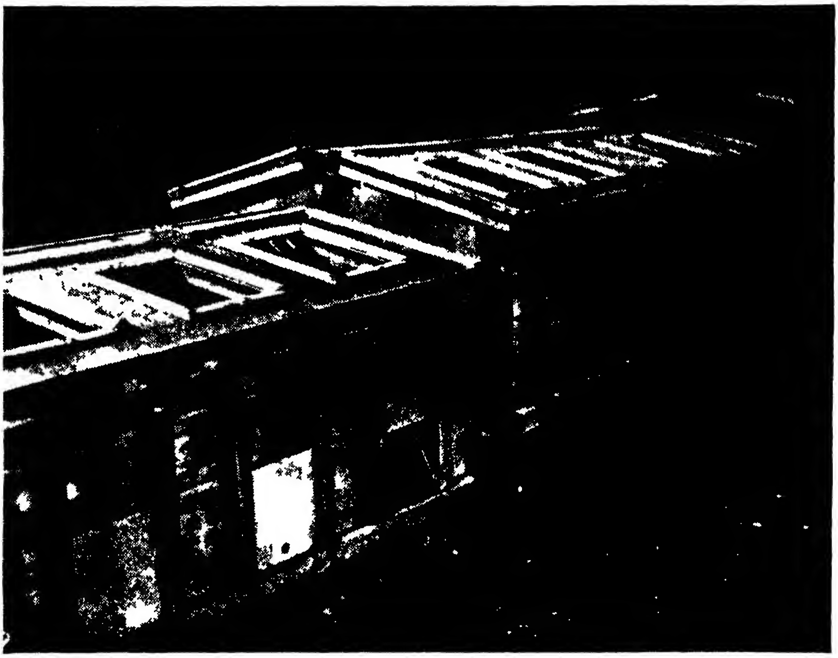

Figure 6.—Trap nests used in Germany in pedigree breeding of ducks for egg production.

contests. Many individual duck records of over 300 eggs per year have been made, while the highest individual production runs over 360 eggs. The use of the single-pen system or of trap nests for keeping records of individual ducks goes back only about 16 years in England, but great progress has been made in improving egg production during these years. Considerable inbreeding has been used, and pedigree breeding and the keeping of production records have been practiced. Progeny testing offers an opportunity for still greater improvement in breeding for egg production.

Improving Size and Color of Eggs

Size and color of duck eggs are inherited so that, where individual records are kept, careful pedigree breeding and selection will lead to material improvement. It is desirable to maintain good egg size in both the egg and the meat breeds. Considerable variation occurs in the color of duck eggs, which have a tendency to show various shades of green. This is natural, since the wild mallard produces eggs with

green shells. Shell colors range from white for the Pekins and well-bred Indian Runners to green for Rouens and dark green or black for the Cayuga. When the Cayuga and Black East India ducks begin to lay, their eggs are almost black, but as production increases the eggs gradually lose their black color and become dark green. White-shelled eggs are desired for market and the popular egg breeds show the great improvement that has been made in selecting and breeding for white eggs. Duck eggs produced by farm flocks on range, which are poorly fed, are not considered to be of as good a flavor as duck eggs produced from well-managed flocks.

Ducks offer a virgin field for poultry breeding research, especially for the inheritance of meat characters, since ducks are used almost exclusively for meat.

GENETIC RESEARCH

VERY LITTLE information has been reported on the genetic composition of the domestic breeds of ducks. The principal plumage-color-inheritance work in this country has been conducted by R. G. Jaap at the University of Wisconsin. A few other research reports on the breeding of ducks will be found in the list of references. Jaap studied the inheritance of three types of white spotting. Two of these types were found to be simple recessive and the third type exhibited incomplete dominance. The dominant type of white markings is found in the Fawn and White and the Penciled Indian Runner varieties and is due to the homozygous expression of a dominant type of white spotting, *RR*, designated "runner." The two recessive types of spotting are found in ducks having white primary wing feathers. One class is due to the heterozygous expression of the genes for runner, *Rr;* the other to a recessive gene, *w*, for white primaries.

Jaap also reported on three allelomorphic genes which produce differences in the mallard-plumage pattern. These three alleles are restricted mallard color, *Mr*, mallard, *M*, and dusky mallard, *md*. Another article describes the effects of a recessive gene which produces a light color phase in mallards. In the juvenile feathering, in the adult plumage of the female, and in the summer plumage of the male the light-phase gene produces a lighter color tone in the ducks that are genetically restricted mallard color, mallard, or dusky mallard color During the summer the adult Rouen male takes on a drab plumage similar to the plumage of the female. After the fall molt the male again assumes his normal bright-colored plumage. Young drakes also have this drab female coloring before they take on their adult plumage.

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THE BREEDING OF FUR ANIMALS

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THE science of breeding can play an important part in conserving and developing the fur resources of the United States in two vital ways. (1) Research is needed to throw light on the breeding habits and gestation periods of wild fur animals so that an intelligent conservation program may be based on the biological needs of the animals concerned. (2) As in the case of domesticated livestock, breeding research is needed to give a more certain foundation for the production of fur animals in captivity—notably the silver fox and the mink. To state which of these two fields is the more important is difficult. Without a vigorous conservation program based on sound scientific knowledge there is great risk of completely wiping out one of the oldest of the valuable resources of the country. On the other hand, fur farming is rapidly becoming an important farm enterprise, and if it is to develop its full possibilities, further information is greatly needed at various points. The industry is all the more significant because it does not compete with any other kind of farming and it utilizes land that is of little or no value for any other crop.

A brief backward glance will show what has happened to the fur resources of the United States to make conservation in the wild so essential and propagation on fur farms a lucrative undertaking of such great promise. In almost every civilization furs have been among the most valued articles of commerce. This was true among the Chinese 3,500 years ago, and later among the Greeks and the Romans. In medieval Europe fur was a luxury much sought after—and incidentally, men made greater use of it for clothing than did women. It was not until after the discovery of North America, of course, that the world fur trade really got into its stride. That it early became an enormously profitable business on this continent is attested by the fact that an Indian trapper could often be induced to part with his winter's catch, worth hundreds of dollars, for a blanket or two and a bottle of rum—and perhaps not very good rum. Among the great fortunes amassed in this game the outstanding example is that of John Jacob Astor.

In these circumstances, with pelts readily obtained and profits large, no attention whatever was paid to the question of the possible exhaustion of this source of wealth that nature distributed with a prodigal hand. The more furs there were on the market, the more popular furs became. The luxury of the rich became the necessity of the moderately well to do. The trap lines were run not less but more intensively, to the profit of everyone—the professional trapper, the landowner,

the farmer who could turn a few extra dollars without much trouble, and a large army of wholesalers, factory owners and workers, and retailers and their employees.

Naturally a depletion of fur resources resulted. This cannot be attributed, however, entirely to overeagerness in trapping. The disappearance of the wilderness, natural habitat of the fur-bearing animals, was a major factor. Nevertheless, even today the trappers and fur farmers of the United States receive $60,000,000 a year for the raw furs they bring to the market. The annual retail turn-over is several times that amount; in 1929, the peak year, it reached half a billion dollars. The United States is in fact the largest consuming market in the world.

PRODUCTION AND DEMAND FOR FURS

TODAY, instead of the United States being the world's chief source of fur supply, this country does not produce enough to meet more than a third of its own demand. Twice as many foreign as domestic furs are now being used in this country, and the demand is increasing rather than decreasing To meet this demand, trappers still take fur animals from the wild with the same extravagant disregard of maintaining or increasing whatever supply is left. It is unquestionable that our natural fur resources will be completely exhausted, unless measures are taken to strike a proper balance between supply and demand.

In this connection there is much need for greater knowledge regarding production. At present no one knows what would constitute

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BEFORE *the development of fox farming there apparently occurred in the common red fox two distinctly different mutations to black (silver)—one among foxes in Canada, giving rise to what are now called standard silvers, and one among foxes in Alaska, giving rise to Alaskan silvers. Beginning in 1928 the Bureau of Biological Survey conducted research to determine the inheritance of the major color types, and B. L. Warwick and the late Karl B. Hanson worked out a hypothesis according to which two dominant genes, A and B, and their recessives, a and b, accounted for all the principal color variations. The results of experimental crosses and an analysis of a large number of litters from recorded matings made by fox farmers substantiated this hypothesis. By referring to a simple genetic chart, it is now possible to determine the expected results of any method of breeding the nine basic combinations of these two pairs of genes. This research indicates the possibilities in the study of the inheritance of fur color, which is of primary importance in fox farming.*

a proper balance. We do not know, for example, whether we are producing 10,000,000 muskrats a year and trapping 13,000,000 or producing 5,000,000 and trapping 25,000,000. We can be pretty sure that we are trapping more than we are producing; but it is important to find out how many more. Almost every State has some fur resources that are a source of income for some of its citizens. The methods of handling these resources are almost entirely haphazard, and in fact few State game and conservation commissions have given sufficient serious thought to the matter. In most States there is no provision for keeping a record of the furs taken each year. In the case of some of the most valuable fur bearers—martens, fishers, wolverines, and otters—the situation has become so serious that the Bureau of Biological Survey has appealed to all State game and conservation commissions to protect them with a 5-year closed period, as the only way to forestall their extermination.

REPRODUCTIVE CYCLES

THE usefulness of breeding data in this situation may be illustrated by the case of the marten (fig. 1). At its experiment station near Saratoga Springs, N. Y., established in 1923, the Bureau has been studying the breeding and the gestation period of the marten. As a result it has found that a period of 9½ months elapses between the time of copulation and birth. With so long a period of gestation, many pregnant females are bound to be destroyed under the prevailing system of open and close seasons. It is obvious that unless the trapping season for a fur animal corresponds accurately with its gestation-free period, the close season will not accomplish what it is intended to: the prospective generation will be destroyed along with the one trapped. Even this precaution, however, would be ineffective in the case of the marten or the fisher, for their gestation periods are too long. A 5- or 10-year closed period is necessary to prevent local or even general extermination of these two fur animals.

The available information on the reproductive cycles of the wild fur-bearing animals is very meager. A review of the literature shows that very little research has been conducted to determine their actual breeding seasons, postnatal development, and gestation periods. Practically all that is now known has been learned by observing the living animals. Few investigators have studied actual embryological material. The one outstanding contribution to the embryological science of fur animals is that of Hartman,[1] of the Department of Embryology, Carnegie Institution of Washington, at Baltimore, Md. This paper presents a study of the physiology of growth and reproduction, the embryology, the rate of intra-uterine and postnatal growth, and the breeding season. More information of this kind is vitally important to any programs of conservation, restoration, restocking, or transplanting, as well as to the success of any effort to produce fur species in captivity. Conversely, it is also important in successful control of noxious animals, which should be most intensively hunted throughout the period preceding the arrival of the young. Similarly important is definite knowledge of the molting and

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[1] HARTMAN, C. G. THE BREEDING SEASON OF THE OPOSSUM (DIDELPHIS VIRGINIANA) AND THE RATE OF INTRA-UTERINE AND POSTNATAL DEVELOPMENT. Jour. Morph. and Physiol. 46: 143–215. 1928.

prime-fur cycles, for, with dependable data at hand, trapping may be confined to the time when a given fur has its maximum value. At present this is rather vaguely considered to be the period of cold weather.

This kind of knowledge is fragmentary in comparison with what has been developed in the case of the domestic animals, which have

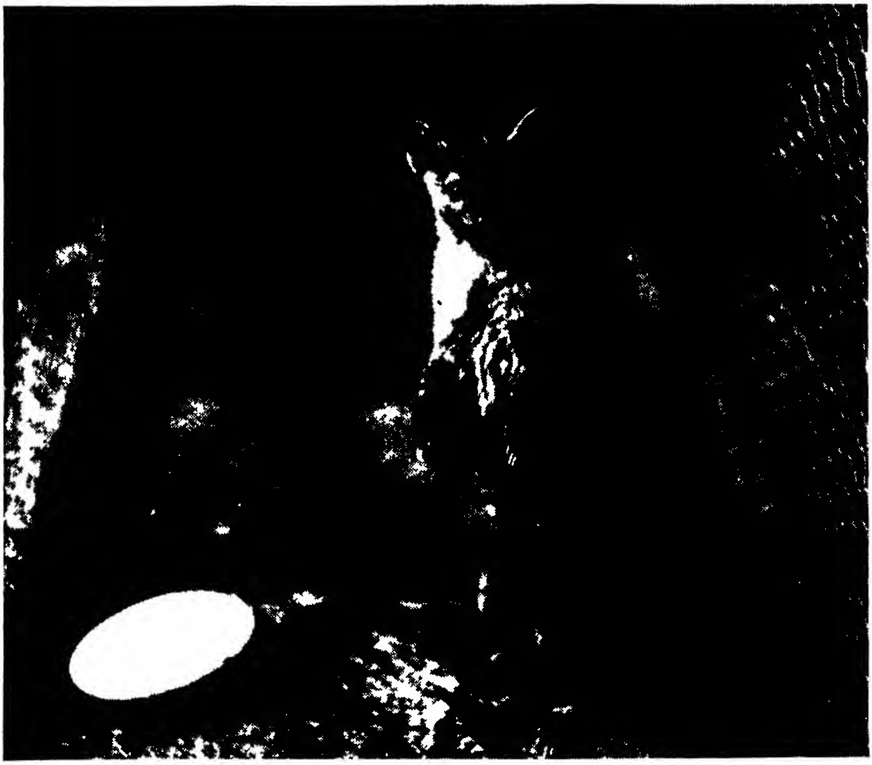

Figure 1.—The marten, one of our most valuable fur animals, is now in danger of extinction.

been under close observation over long periods of time. The place to begin, however, is at the beginning, no matter how elementary it may seem.

RAISING FUR ANIMALS IN CAPTIVITY

Raising animals in captivity as a means of supplying the need for furs is an industry that is both new and not new. The Chinese have for centuries bred sheep, goats, and dogs for their pelts. The outstanding example of a domesticated animal bred specifically for this purpose is the Karakul sheep, which has long been produced for lambskins on the uplands of Bokhara in central Asia. Afghanistan is now perhaps the most important center of this industry, and the annual production of lambskins there is (1936–37) 1,200,000; the

Union of Soviet Socialist Republics is next, with an annual production of 900,000 skins. About 30 years ago Karakul sheep raising was started in what was then German Southwest Africa, and today the farmers of that region are producing annually about 700,000 skins and shipping them to the raw-fur markets of the world. Karakul sheep are also being produced in the United States, but there are few purebred animals in this country. The foundation stock came from small importations from Bokhara in 1909, 1913, and 1914. Further importations are next to impossible. The Federal quarantine regulations prohibit direct importation into the United States, and it is too expensive to make indirect importations by holding the animals for the required length of time in another country.

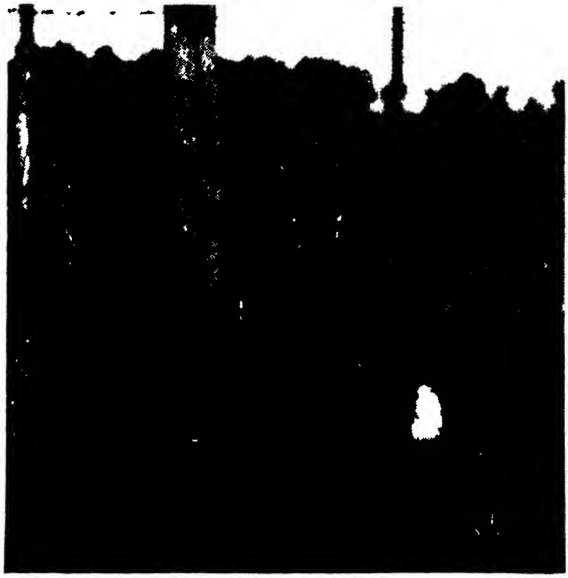

Figure 2.—The production of silver foxes on farms now (1936) exceeds 200,000 annually.

In the face of this situation the Bureaus of Animal Industry and Biological Survey have been cooperating in a breeding experiment that promises favorable results. Since it would be almost impossible to increase the breed to any appreciable extent from present stocks of purebred animals, the Department has been carrying on cross-breeding experiments with Karakul × Black-faced Highland and Karakul × Corriedale at the National Agricultural Research Center, at Beltsville, Md.

The most spectacular and important development in fur-animal production, however, is in silver-fox farming (fig. 2). This development has taken place during the last 40 years, and though brief, the history of the industry has been sensational. Two Canadian farmers on Prince Edward Island, Charles Dalton and Robert Oulton, started to experiment in 1894 with cross and black (silver) foxes, some captured and some purchased. They bred the foxes in captivity and finally obtained some entirely black and silver puppies. The neighbors soon learned of their secret operations and before long several fox farms were established on the island. It was generally understood that Dalton and Oulton were making money, but it was not until the 1910 sales figures were published that the extent of their profits became known. In that year they received for 25 pelts an average price of $1,339. One pelt brought the all-time high price of $2,627. This started a fox-farming boom and sent the prices of

breeding stock skyrocketing. The boom collapsed at the beginning of the World War in 1914, but in 1923 people were again investing anywhere from $500 to $5,000 per pair in foxes, which in some cases they had never seen. By 1927 the unhealthy speculation in breeding stock had died out and ranchers went to work producing the animals for the fur.

Production on Fox Farms

Fox farming today represents the greatest development thus far in raising fur animals under strictly controlled conditions. It can still be considered a relatively new industry, however, since practically all the development in production has taken place since the World War. The number of pelts produced and sold in the United States is estimated to have increased from 6,000 in 1923 to 200,000 in 1935. The total value of the sales increased from $819,429 in 1923 to $7,719,600 in 1928. During the next 3 years prices declined because of the depression and the increased production of skins, but from a low point of $3,472,200 in 1931 they advanced to $7,114,500 in 1934.

Foxes are grown successfully throughout the northern half of the United States, from New England westward to Washington and Oregon, and in the cooler parts of California. The greatest numbers of silver foxes are produced in Wisconsin, Minnesota, and Michigan, and these three States are contributing more than 50 percent to the annual crop of pelts. The largest two companies in the world producing silver foxes operate in Wisconsin. Each maintains about 7,600 breeding pairs. The other principal fox-farming centers are in the Rocky Mountain region, including Oregon and Washington, and in the New England States, Illinois, Ohio, New York, and Pennsylvania.

In Canada, fox farming has had a development similar to that in the United States but on a somewhat smaller scale. In 1923 sales of pelts from Canadian fox farms were slightly greater than in this country. In 1935 the number of Canadian pelts sold totaled 120,465. Furs from farms now play an important part in the fur trade of both Canada and the United States. The value of the pelts from farm-raised animals represents approximately 31 percent of the total annual value of the raw-fur crop in the Dominion and 20 percent in the United States.

Abroad, fox farming has had a phenominal development, particularly in Norway, where the industry has grown like a mushroom. During the season 1934–35 the number of pelts produced was 103,604. Other European countries also are producing silver foxes, and in Japan and South America the industry is well established. The European silver fox pelts, especially those from Norway, must now be considered an important part of the world supply. If silver fox farming develops extensively in South America, the farmers of that continent will have a seasonal advantage in getting the pelts to the markets, for pelting there is in July and August

The world production of silver fox pelts for the season 1935–36 was probably in excess of 500,000 distributed approximately as follows: United States and Canada, 350,000; Norway, 125,000; Sweden, 25,000; Netherlands, 5,000; Denmark, 3,000; Union of Soviet Socialist Republics, 4,000; Germany, 3,000; England, France, Switzerland, Japan, and South America together, 3,000.

It can hardly be doubted that this comparatively new fur-farming industry has become a permanent part of our agriculture. It has met with relatively more success in recent years than most other branches of agriculture, and it promises still greater developments when freed from the artificial restraints and handicaps that at present are retarding its progress. Fur farming fits in well as a side line to general farming

Figure 3.—Many small fur farms like this one in Massachusetts are producing fur as a side line to other agricultural pursuits.

because it can utilize certain parts of the farm not adaptable to growing other crops. It also provides a winter occupation and brings in additional revenue during the season when both are needed to balance farm operations.

In 1926, when the annual production of silver fox pelts in the United States was about 25,000 and the average price for skins was $126, farmers began to worry about the possibilities of overproduction. Many were wondering whether increasing production of furs year after year would not outstrip even the increased demand, including that resulting from the normal population increase. At that time the prices paid for pelts were dropping and the cost of feed was going up. The situation at that time was more alarming to the small than to the large producers.

Today, a decade later, the annual crop of pelts has multiplied eight times, to 200,000. Silver fox fur is fashionable, in fact very fashionable. The average price for raw pelts has dropped to $42, only a third of that realized in 1926. Food costs are increasing rapidly. Some fox farms have grown bigger, others better. Conditions now are not perplexing so much to the small as to the large producers. The reason for this change is that the former does not have all his eggs in one basket—pelt production with him is a side line (fig. 3). Furthermore, pelt production costs him less on the average than it does the

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large producer and the price he receives for a pelt is on a par with that obtained by the latter. The small producers as a group are today marketing more than 140,000 pelts each year, while the large producers contribute only 50,000 or 60,000 to the annual crop.

Experiments with Other Species

Minks, martens, fishers, skunks, raccoons, and opossums also are being raised in captivity to some extent, the most striking developments having been in mink farming. The number of farm-raised

Figure 4.—Skunks are easily raised but not at a profit.

mink pelts has increased rapidly, and the prices paid have been exceptionally good, reaching their high point during the 1936 season. These favorable conditions have naturally stimulated expansion. Generally speaking it may be said that in the case of fur animals other than foxes and minks more money is invested in feeding, breeding, and management than can be realized from the sale of the pelts. For the present, at least, the production of skunks (fig. 4), opossums, raccoons, martens, and fishers for fur is not a profitable undertaking.

The problems of the fur farmer are fundamentally the same as those of other producers of livestock. They include a knowledge of his animals, their physical needs and temperament, and the requisites of sanitation, feeding, breeding, and disease control. In all of these lines, scientific research has a part to play, but so far research has been of very limited extent.

Present Breeding Methods

During the relatively short period that foxes have been raised by man no particular strains of outstanding characters have been developed. The best of them, however, produce fur of high quality. The problem then becomes one of producing fur of a given character

and quality with greater certainty. In addition, the fox farmer would like to be sure of getting good producing vixens in order to increase his pup crop; and he would like to have greater control of diseases and parasites, some of which are common to domestic livestock and some peculiar to foxes. The disease problem has been paramount, as the losses on fox farms in certain sections of the country have been disastrous, in some instances entire ranches having been wiped out. The application of veterinary science is aiding in developing the industry, although research has not yet developed methods for complete protection against several diseases that are causing heavy losses on fox farms.

The accumulated knowledge developed by plant and animal breeders should be of great value to fur farmers, but the latter have been slow in applying it to fur-animal production. In the past, time given to promotional schemes for selling breeding stock to unsuspecting buyers was much more lucrative than that devoted to the tedious study of basic principles of fox breeding, feeding, and disease control. Then, too, the rapid shift in the market requirements from dark to full silver pelts has kept the farmers busy—and worried—supplying the demands of fashion.

In their breeding operations, fox farmers have primarily stressed the selection of particularly good, true-breeding types and the use of such animals as breeding stock. Increased prolificacy and the production of fur of high quality have been the main objectives. The fur farmer has not advanced so far as the breeder of domestic livestock in the application of definite breeding principles to his problems. Among fox farmers in general, there is as yet no idea of developing a fox strain different from any now in existence and perhaps possessing outstandingly valuable characters. Such good specimens as have been developed have resulted from continued selections for a few desired types.

Market Requirements

It must be said, however, that the vagaries of fashion have had a good deal to do with the failure thus far to set up certain definite long-time objectives. Forty years ago black fox was popular; a few years later the highest prices were being paid for quarter and half silvers; and during the last 4 or 5 years the full silvers have been setting the upper price limits because they are in keen demand for working into short and long capes, short coats, enormous collars, and wide trimmings on fur coats, cloth coats, and dresses. In 1936 the prices obtained in the United States for full silver pelts were 50 percent higher than in Great Britain.

These shifts in market requirements necessitated strenuous efforts on the part of breeders to satisfy present demands, with a minimum of attention to the future. Charles E. Kellogg made an exhaustive study of the silver-fox-pelt markets of the United States and Great Britain covering the 5-year period 1932–36 to determine the effects of trends on the percentages of silver in the pelts. The results showed that about 36 percent of the American offerings in 1936 were full-silver skins, an increase of 225 percent during the 5-year period.

This demonstrates how quickly the majority of farmers produced the maximum of light-silver pelts. Some cautious breeders, however, are retaining some of the darker silvers in the breeding herd as an insurance reserve, in case there should be a sudden return to the half and three-quarters silvers, which are more satisfactory for scarf purposes. Other breeders feel confident that the genetic make-up of silvering is dependent upon so many factors that persistent selective mating toward darker colors would supply such a new demand just as effectively, though perhaps somewhat more slowly. They feel that their method permits maximum concentration on full silvers for the present higher prices. There are no authentic scientific data available to demonstrate that either method is correct, and thus the producers continue to be faced with an important problem that for the present remains unsolved.

RESEARCH IN INHERITANCE IN THE FOX

It is quite generally appreciated that there is still much room for improvement in the color and texture of silver fox fur. The pelts now coming to the market are generally somewhat better in quality than a year ago, but this is true mostly for individual ranches rather than for sections of the country. Since the number of pelts offered for sale is increasing year after year, buyers are naturally becoming more discriminating, especially with the increased competition that now involves other countries as well as the United States. Fox farmers have reached the point where they must exert every possible effort to improve the quality of the fur produced. For the present, close culling of the breeding stock, which means pelting the undesirables, and intelligent and strict selection of breeding animals are the most certain methods to bring about a marked improvement in fur quality.

To meet the need for fundamental information on the genetic basis of silvering, the Biological Survey began an experiment in 1935 at the United States Fur Animal Experiment Station, at Saratoga Springs, N. Y. An attempt is being made to determine, if possible, the genetic factors involved, so that market requirements can be met more promptly. The objective is to determine the relationships between the various degrees of silvering and to work out methods of breeding that will enable the breeder to have more control over them. Only a small number of foxes is available for this experiment, whereas experience proves that a large number must be used to obtain definite results where many genes are concerned. There has been only one other research program to trace the inheritance of fur colors, and this was concerned not with gradations in silvering but with the basic differences between red, cross, and black (silver) foxes. To make this clear, it is necessary to give a brief account of these different types.

Before the development of fox farming, there apparently occurred in the common red fox (*Vulpes fulva*) two distinctly different mutations to black. One of these, namely, that to which the standard or Prince Edward Island silver fox traces its origin, must have occurred somewhere in Canada, probably in the eastern or central part. The other, to which the Alaskan silver fox traces its ancestry, certainly must have occurred in Alaska, most likely in the interior. The so-called cross fox was probably produced by crossing the red and the silver (fig. 5).

Thus foxes of the genus *Vulpes* may have three kinds of pelts: (1) The common red fox, which is primarily red or fulvous with a mixture of gray or brown except for restricted black markings on the feet and ears, a white area at the end of the tail, and certain white-banded hairs on the back and rump; (2) the typical cross fox, in which black predominates on the feet, legs, and under parts, while red or fulvous overlying black covers most of the head, shoulders, and back; and (3) the black (silver) fox, which carries no red or fulvous, the entire pelage being dark at the base and heavily or lightly overlaid with the banded guard hairs that produce the silvery appearance. These guard hairs are not entirely white but are black with a white band, and some are entirely black. Foxes of the third group vary from animals that are almost entirely silver to those that are entirely black except for a few white-banded guard hairs on the back and rump. The fur trade recognizes five classes of silver fox pelts, graded according to the percentage of silver, as follows: Full, three-quarters, half, one-quarter, and slightly silver or dark.

Figure 5.—Litter of pups resulting from cross-breeding a silver with a red fox.

It is believed that what are called standard silver foxes, carrying a factor for silver and black color, were found naturally in many parts of Canada. Few if any of these foxes migrated into Alaska. On the other hand, the progeny of Alaskan silver foxes, also carrying a factor for the silver and black color, probably traveled southward over the mountain range and spread over a large part of Canada. Neither the Alaskan nor the standard silvers migrated to any extent south of the Great Lakes and the St. Lawrence River. The indications are, however, that some foxes possessing either or both of these factors for silver and black must have migrated or occurred naturally south into the northern parts of the States bordering on the Great Lakes.

In the early days of fox farming, red and cross foxes captured in the wild were bred to produce silvers. As more silver foxes became available, they replaced the red and cross foxes on ranches, and silver foxes were bred together to produce silvers. As time went on foxes that would breed true for silver were developed and it became generally understood that silver foxes produced from silver fox parents would always breed true. Later on, however, when silver foxes originating in Canada were bred to silver foxes from Alaska, the young produced proved to be crosses and not silvers.

Genetic Relationships Between Red, Cross, and Black Foxes

Prior to 1928 no scientific research had been conducted to determine the genetic basis of the red, black (silver), and cross coloring in foxes, and consequently there was considerable confusion as to the genetic relationship between the black color in standard and in Alaskan foxes. In 1928 it was decided to include such studies in the program of research for the United States Fur Animal Experiment Station. B. L. Warwick, of the Texas Agricultural Experiment Station, cooperated with the late Karl B. Hanson, of the Fur Animal Station, and proposed a hypothesis that would account for the results obtained. To clarify the discussion somewhat, this hypothesis will be given first. Warwick suggested that genes *A* and *B* and their alternative forms (alleles) *a* and *b* account for red, black (silver), and cross colors in foxes. All the possible combinations of these genes would give the following types:

AABB=Alaskan red.	*AABb*=Smoky red.	*AAbb*=Standard black (silver).
AaBB=Cross.	*AaBb*=Blended cross.	*Aabb*=Substandard black.
aaBB=Alaskan black (silver).	*aaBb*=Sub-Alaskan black (silver).	*aabb*=Double black.

Hanson found that when the standard black and the red foxes were crossed, the offspring were usually a smoky red. Although red was strongly dominant to black, it was not completely dominant; there was some blending that produced the smoky color. Foxes of the first filial generation had larger prominent dark points and more evidence of black than is usually present in the red parents. Segregation into reds, smoky reds, and blacks occurred when the first-generation offspring were bred inter se, that is, bred to their own kind. The ratio of segregation was about 1 red to 2 smoky red to 1 black. When smoky red foxes of the first filial generation were backcrossed to the black parents, the result was a ratio of 1 smoky red to 1 black. These ratios indicated that a single gene accounts for the difference between pure standard blacks and reds.

On some fox farms, however, where supposedly pure standard black foxes were bred with pure red ones, mixed litters of smoky reds and reds in about equal proportions were produced in the first generation. Doubtless the black (silver) parents were not pure but had a hybrid combination of the genes *A* and *a*.

Some red foxes caught in the wilds of Canada, the Upper Peninsula of Michigan, and northern Minnesota and Wisconsin when crossed with pure standard blacks produced mixed litters, with blacks and smoky reds in equal proportions. If these wild red foxes were really hybrids or smoky reds, it would account for the results.

When Alaskan blacks were crossed with red foxes, the first generation were all cross foxes, but no appreciable dominance of black or red was in evidence. When the first filial generation was bred inter se, there was a segregation of 1 red to 2 cross to 1 black (silver). The cross foxes when backcrossed to black parents again produced crosses and blacks in equal proportions. The ratios again indicated a difference of one gene between pure red and pure Alaskan silver foxes.

Hanson then crossed Alaskan and standard black (silver) foxes. The first filial generation turned out to be blended cross foxes. This

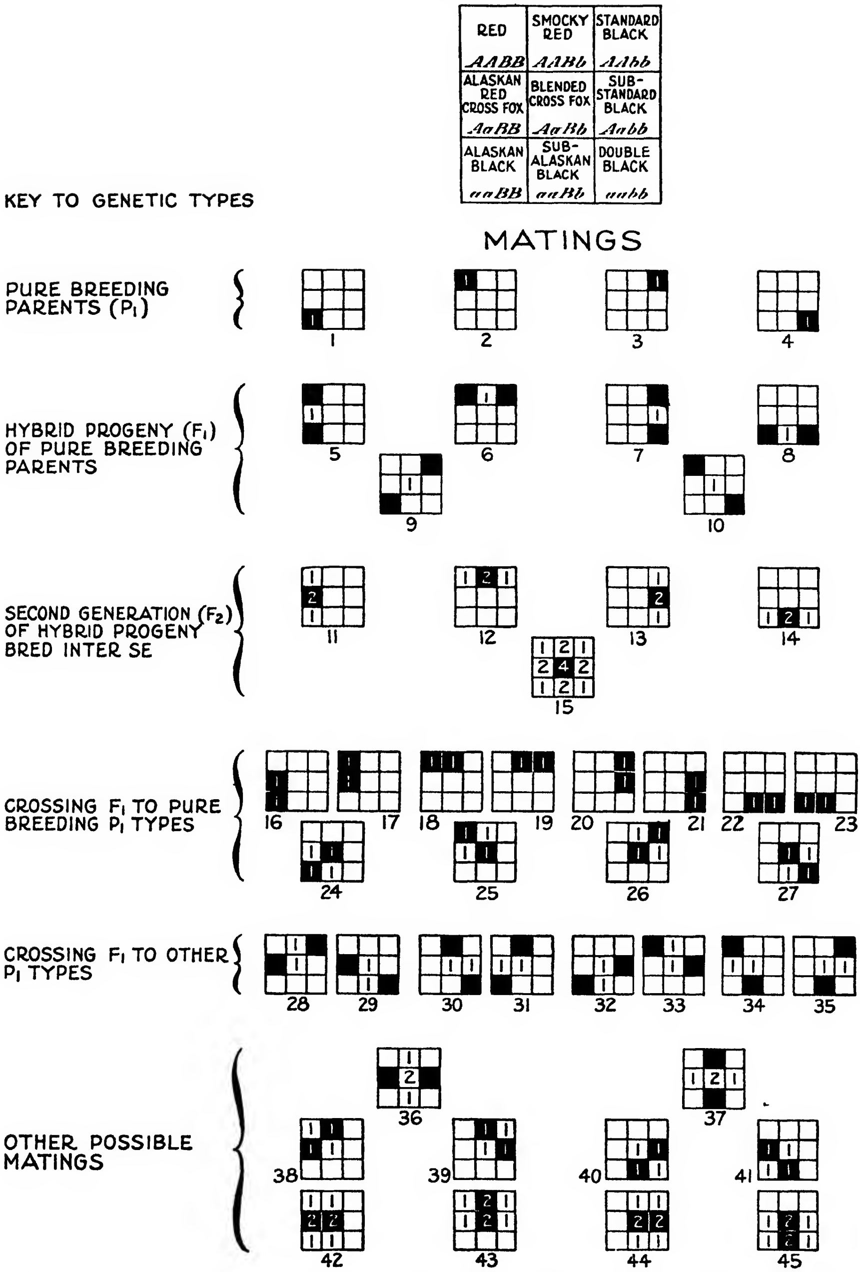


Figure 6.—**Diagram illustrating the genetic types of foxes and the results of various matings on the basis of a two-factor inheritance. Black squares represent matings, and numerals within the squares represent the expected distribution of progeny in proportions.**

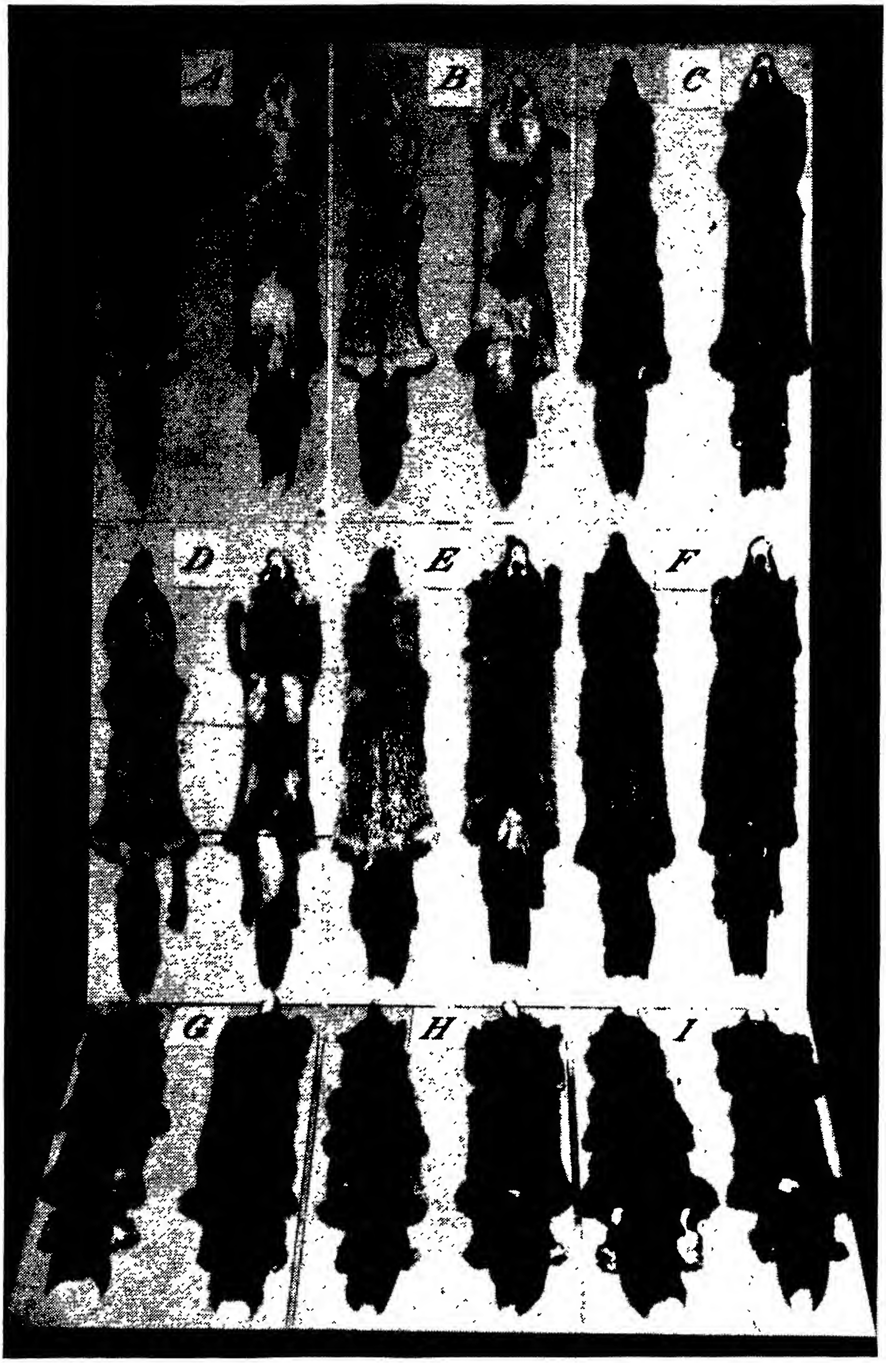


Figure 7. (Legend on opposite page)

indicates that two different genes are involved in Alaskan and standard black foxes.

In some instances when Alaskan blacks and standard blacks were mated, black young occurred in the litters. Check matings demonstrated that the occurrence of black in the first filial generation was due to the fact that one or the other of the parents was not pure but hybrid for either *A* or *B*.

Inadequate facilities and lack of funds made it impossible to maintain a sufficient number of foxes at the Fur Animal Station to make a complete investigation of this kind. Therefore, the research workers had to solicit the cooperation of fox farmers who had been conducting cross-breeding experiments in the United States and Canada. They willingly furnished the data obtained from their breeding operations, and these proved to be most valuable in amplifying the results obtained at the experiment station.

Hanson made a biometrical analysis of these data and found that three principal colors in foxes are inherited in accordance with the factor hypothesis previously mentioned. In 775 litters, including over 3,000 pups, representing 30 different combinations of types, only 4 litters were reported in which the results were contrary to the hypothesis. In at least two of these cases there was some doubt as to whether the vixen was served by two different males or whether the parents were improperly classified as to color.

Hanson designed a chart to illustrate the results of the various matings on the basis of two-factor inheritance (fig. 6). At the top of this chart is a key to the three different colorings and the nine different combinations of genes that result in nine different types. Directly under the key is a series of smaller nine-block squares giving the 45 different mating combinations of these nine types. The black squares in the blocks represent the genetic types mated and the numerals represent the expected distribution of progeny in proportions. Reference should be made to the key at the top of the chart to determine the colors (fig. 7) and genetic make-up of the animals being mated and also the progeny.[2]

As examples of the use of the chart: Suppose Alaskan blacks are to be mated with standard blacks. This mating is given in the set of

[2] In matings producing more than one kind of progeny the result may deviate in the distribution of progeny in individual litters or in a small number of litters, not only among foxes but among other animals also. For example, the expectation from crossing a substandard black with an Alaskan black (fig. 6, square 32) is that the progeny will consist of blended crosses and sub-Alaskan blacks in a 1:1 (50:50) ratio. As likely as not, this mating will produce an equal number of crosses and blacks (silvers). The probable occurrence of different combinations of cross and black foxes in litters of four thus produced is as follows:

Black (silver) foxes	4-3-2-1-0
Cross foxes	0-1-2-3-4
Total	4-4-4-4-4

Although these figures represent the proportion of black (silver) and cross foxes that may occur in litters of four, litters of that size do not always occur. In sufficient numbers there would be produced six times as many litters containing equal numbers of silver and cross foxes as there would be litters of all silvers or all crosses. Likewise the litters with three pups of one color and one of the other would be produced four times as frequently as would be litters of all one color.

Figure 7.—Fox pelts of the nine genetic types, upper and under side illustrated in each case, and grouped as in the square diagram in figure 6: *A*, Red, *AABB; B*, smoky red, *AABb; C*, standard black, *AAbb; D*, Alaskan red cross fox, *AaBB; E*, blended cross fox, *AaBb; F*, substandard black, *Aabb*; *G*, Alaskan black, *aaBB; H*, sub-Alaskan black, *aaBb; I*, double black, *aabb*.

squares numbered 9. The figure 1 in the middle square indicates that all the progeny will be blended cross foxes. Now suppose these blended cross foxes are bred together, as in the set of squares numbered 15. The figures in the squares indicate that every kind of fox will result from these matings, and that in a large number of matings the proportions may be expected to be 4 blended crosses, 2 Alaskan red crosses, 2 smoky reds, 2 substandard blacks, 2 sub-Alaskan blacks, 1 red, 1 standard black, 1 double black, 1 Alaskan black. If an Alaskan black is mated with a smoky red, as in the set of squares numbered 31, the result will be 1 Alaskan red cross to 1 blended cross. If a sub-Alaskan black is mated with an Alaskan red cross, as in the set of squares numbered 41, the result will be equal numbers of Alaskan red crosses, blended crosses, Alaskan blacks, and sub-Alaskan blacks.

A SUGGESTED PROGRAM FOR FURTHER RESEARCH

Fur farmers look to the scientist for leadership in the development both of basic information in fur-animal breeding and of methods of improvement, and they have appealed many times to the Federal and State Governments for assistance Little has been done, however, by public agencies to develop this new and promising animal-production enterprise, and there has been no systematic effort on the part of State agricultural experiment stations or the Department of Agriculture to develop, isolate, perpetuate, or record fur animals of superior breeding ability.

In order to place fur farming on a foundation comparable with that of other branches of agricultural production, fundamental knowledge is essential, and this can be obtained only by inaugurating a comprehensive program of research. Such a program might be conveniently divided into three parts:

1. Research work on reproductive cycles. Most of the study thus far has been concerned with domestic species, and the available definite information on wild animals is very meager, particularly as regards species of economic importance. A more exact knowledge of the reproductive cycles of North American fur animals could be applied in several ways. It would be of great value—(a) in determining the proper trapping seasons for restoring and conserving fur animals; (b) in attempting intelligently to supplement the natural supply by restoring and transplanting; (c) in insuring success in producing fur species in captivity; and (d) in making possible a more efficient and economical control of predatory and other injurious species. The object of research on reproductive cycles would be to establish definitely—(a) the breeding period of valuable fur animals; (b) the number of litters and young produced yearly; (c) the type of embryonic development (whether uninterrupted or with a delay in implantation); (d) the hormone control of the breeding cycle; (e) the feasibility of artificial insemination in those species that might be raised in captivity; and (f) possibilities for producing or maintaining reproductive fertility by hormone or other treatment.

2. Breeding experiments with various fur animals under controlled conditions. These should be conducted to study the inheritance of prolificacy and fur quality, which includes color, sheen, and density.

In all animal breeding it is vital to concentrate on as small a number of objectives as possible. Measurements must be devised to evaluate all these characteristics with greater certainty, especially fur quality. Similarly, there should be measurements for efficiency of feed utilization, since the cost of feeding is a large part of the cost of production. Where genetic factors (genes) might be directly useful, as in the case of coat colors, they should be determined so far as possible. They will doubtless prove to be extremely complex, but the research on color inheritance already described indicates that something may be done to segregate definite traits of this kind and to breed for them. Meantime, to use breeding stock of proved performance, as determined by the progeny test and by dependable records of parental characteristics, would be to approach the problem in the way that has proved to be of such great value in other branches of livestock breeding.

3. Attention to nutrition. This article is concerned primarily with breeding and genetic research, but in any comprehensive research program, nutrition is equally important. Practically no fur-animal research studies have been conducted on digestion and metabolism, the chemical composition of foods, and the part played by various foods in growth, fattening, maintenance, reproduction, and the economical production of pelts of high quality. With few exceptions, all fur animals are meat eaters. The maximum and minimum quantities of red meat that can be fed during the various stages of development should be determined. Some work has been done to determine the value of cereals, vegetables, and protein supplements in the ration, but it should be expanded. These and many more nutritional problems when adequately solved will enable fur-animal breeders to proceed more surely, safely, and efficiently.

Without extensive controlled experiments, all breeding and feeding practices are of a hit-or-miss nature. But experiments with fur animals are exceptionally costly, not only in the matter of equipment, but also in the time involved, for breeding stocks are expensive and practically all species produce only one litter a year. In addition, scientific training and the ability to conduct research are required, and the economic results of any given project are by no means certain. Private breeders therefore are not likely to do much experimenting, because they must confine themselves to operations that are fairly certain to produce immediate profits. Fur-farmers' organizations or wealthy producers might undertake some forms of research work, but men change their minds and associations change their policies, and under these conditions there is no assurance of continuity. There are many reasons why fur-animal research must be conducted primarily by properly equipped public institutions, but this can be done only in response to a sufficient public demand and with the active support of those who have a stake in the industry.

BEE BREEDING

W. J. NOLAN, Apiculturist, Division of Bee Culture, Bureau of Entomology and Plant Quarantine

THE economic importance of bee breeding, measured in dollars, is probably greater than is realized even by the beekeeper. The potential stake of agriculture in the United States in queens alone is over $2,000,000, if a value of 50 cents, the minimum price set by the marketing agreement governing the sale of queens, is placed on each of the

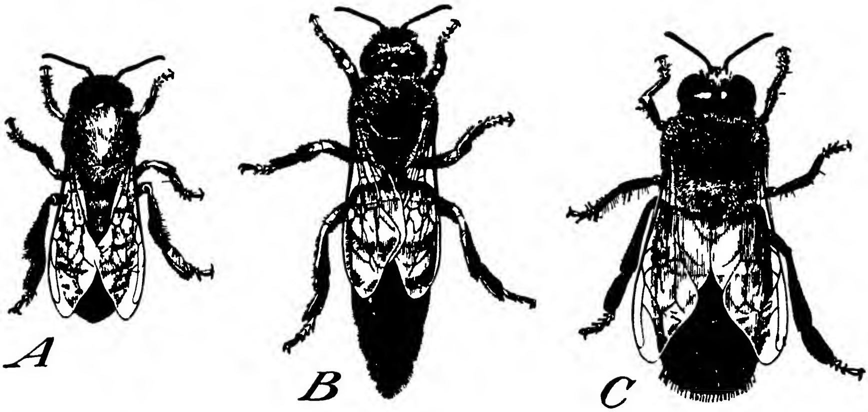


Figure 1.—The three inhabitants of the hive: *A*, The worker, a female with arrested development of the egg-laying organs; *B*, the queen, a female with completely developed egg-laying organs but with undeveloped secondary sexual characters such as those possessed by the worker for secreting larval food, for gathering nectar and pollen, for secreting wax, and the like; *C*, the drone, the male bee. During the height of the season, a bee colony may consist of several thousand workers and a few hundred drones, but it normally contains only one queen at any time.

queens in the more than 4,000,000 colonies of bees in this country. The amount invested in bees, hive and honey-house equipment, and the like is $35,000,000 to $50,000,000 on the conservative basis of $8 to $12 per colony. Whether a fair return is being received by the beekeeper on these sums, plus the amount involved for his time and labor, depends primarily on the blood represented by the queen and by the drone with which she mates (fig. 1).

The public is also directly affected by the breeding problem, not merely from the standpoint of being insured an abundant supply of honey, but from the more important standpoint of having bees that will function as efficiently as possible in the pollination of many of

our crops. For example, clover crops, which are so fundamental in the dairy and livestock industries, apples and other fruits, and truck crops in greenhouses are now more or less wholly dependent on the efforts of the honeybee. There is interest also in increasing the supply of native beeswax, which at present comes so far short of meeting domestic demands that large quantities are imported annually. The bee is far more valuable to American agriculture through all these other activities than through its honey production. As a matter of fact, the activities of the honeybee are so varied and so useful that practically every person benefits by them in some way or other, and so will benefit, indirectly at least, by any improvements that result from scientific breeding.

FACTORS LIMITING PROGRESS OF THE BEE BREEDER

In spite of its importance, bee breeding is only in its infancy, one reason being that promising methods for mating queens and drones under laboratory conditions had not been worked out until within the last few years. Prior to the development in 1923 of the Quinn-Laidlaw technique discussed later in this article—whereby, through the agency of the operator, the drone organ is everted in proper position in relation to the queen for insemination to take place, and in

SEVERAL *desirable characters have been commonly recognized among the varieties of honeybees used in the apiary, but the breeder during past years has been able to do little in combining these in one bee because in nature queen and drone mate only on the wing. These characters have to do with disease resistance, color of comb cappings, size of body parts, constancy of color markings, disposition, and swarming propensity. Because of recent work that shows the feasibility of accomplishing the insemination of queen bees by laboratory methods, the breeder is now in a position, however, to utilize the characters already available in the germ plasm of bees and to start at once toward the goal of breeding bees better adapted to present agricultural demands. It would be a great and perhaps not impossible achievement to breed a bee with the long tongue of the Caucasian, capable of reaching sources of nectar not now available to most honeybees; the gentleness of the Caucasian and the Carniolan; the white comb capping made by the black bee and the Carniolan; the reduced swarming tendency, and the resistance to common hive enemies and European foulbrood, of the Italian; the uniform marking of the Cyprian; and the industriousness of the Italian or Cyprian.*

1926 of the Watson technique for the artificial insemination of queen bees through the transfer of sperm from drone to queen by means of a microsyringe (fig. 2), the bee breeder was forced to trust to luck in his work, because he had to rely on chance natural matings in midair, since in nature the honeybee mates only while on the wing away from the hive. A successful method for obtaining natural matings of queen and drone in confinement still remains to be developed.

Figure 2.—L. R. Watson, who developed the Watson method for the artificial insemination of queen bees, seated at his instruments.

Another reason for the backwardness of bee breeding is the fact that only since the application of biometric methods in studying the body parts of individual bees, a development of recent years, has progress been made in working out a method whereby the breeder can readily identify the race or strain with which he is working. Mendel, the father of modern genetics, lacked a means of distinguishing between strains when he endeavored to work out problems of bee genetics in addition to those of the genetics of peas, which brought him fame (*9, pp. 142–157*).[1]

The first investigator to make a comprehensive biometric study of the honeybee was Kozhevnikov (*12*), who in 1900 endeavored to separate the various races on the basis of physical measurements made with the aid of a microscope. He included such measurements as hooks on the wing, tongue length, length of leg segments, length of abdominal segments, length of wings, and the like. Since that time Russian investigators have been particularly active in this field.

However, the problem of checking differences between various crosses, strains, and races of the honeybee on the basis of the physical characteristics of individual bees, or even of the productivity of colonies, and then utilizing the results in breeding, is far more complicated than with other farm animals. This is due not only to the small size of the honeybee, but also to the fact that honeybee productivity represents the collective efforts of the thousands of individuals making up a colony. It is even hard to define a standard colony for purposes of any comparative experiments, since, even under the same natural conditions outside the hive, within the hive the physiological ages of the individual bees differ. Furthermore, the honeybee cannot carry on its life functions indefinitely in confinement, as can cattle, poultry, rabbits, or even pigeons.

Advances in scientific bee breeding are also limited by the variety of demands on the breeder. Queens must be reared and tested; drones must be reared; mating of queen and drone must be accomplished;

[1] Italic numbers in parenthesis refer to Literature Cited, p 1537.

progeny must be tested for colony characteristics and production, as well as for physical characteristics of individuals; and results must be evaluated. The scientific breeder should possess a working knowledge of the biology of the honeybee, including an intimate knowledge of its various races and strains, and of genetics, biometrics, and supplementary fields as well. In short, he should be a combination beekeeper, laboratory technician, biometrician, and geneticist, or know how and where to utilize the services of specialists in the various fields involved.

Another situation faced by the bee breeder is the fact that worker bees cannot be bred, and the queen and drones, mating but once in a lifetime, cannot be used in line breeding involving parent-offspring crosses. Furthermore, since queen and drone function only in reproduction, progeny tests—in other words, the collective colony behavior exhibited by the worker progeny—must be relied upon exclusively in testing the inheritance of the queen and drone for such economically important characters as honey gathering, wax secretion, pollinating activity, and the like. Even when a parent queen is bred pure for the same color factors as the drone with which she mates, her color pattern may differ from that of her worker daughters, since in some races, the Italian being one, the causes that lead to the development of worker structures in a larva, with a resultant arrest in the development of its reproductive organs, also lead to a modification of its color pattern.

MORE KNOWLEDGE REGARDING REPRODUCTIVE PROCESS NEEDED

The advantageous employment of present mating methods, or their improvement, whether natural or artificial insemination is involved, will be facilitated when the physiological processes preceding and accompanying mating are better understood, since much remains to be known regarding the conditions most favorable for mating. For example, the consensus of opinion is that the queen mates when about a week old or shortly thereafter, but a queen 56 days old has been artificially inseminated with success. A knowledge of the external signs, if there are any, that queen and drones are ready for mating should go far in increasing the usefulness of methods of artificial insemination and also be of advantage in work involving natural insemination.

As a matter of fact, until recent years little was known about reproduction in the honeybee. Knowledge that drones are produced from unfertilized eggs (parthenogenesis), at least in European varieties of the common honeybee, dates only from the middle of the last century, and the origin of queen and worker and the fact that the queen mates on the wing outside the hive has been known for only about 150 years.

More has been done in studying the mating processes in the drone than in the queen. The most complete study on the drone is that by Bishop (*4*), who found that usually the drone is not sexually mature until the ninth to twelfth day after emergence, but that some drones are apparently incapable of mating at any age. Bishop also found the function of the mucus, which the male organ contains in addition to sperm. During mating the sperm is merely transferred from the

drone to a temporary storage place in the vagina and oviducts of the queen. The spermatozoa collect within the spermatheca during the next few hours and may live there for 6 years or more. While still in the oviducts and vagina, however, the sperm might all escape through the genital opening were not this opening filled with the mucus from the drone when the last of the sperm has entered. This mucus quickly hardens on exposure to air, and thus forms a temporary stopper in the genital opening.

The anatomy and the physiological responses of the queen in relation to mating are being studied by Harry Laidlaw, formerly in the employ of the Department but now a graduate student at the University of Wisconsin. This study includes the structure and functioning of the queen's genital organs, a subject on which little is known, but a knowledge of which is demanded for the further successful development of methods, not only of artificial insemination but even for obtaining natural matings in confinement. Laidlaw has found that a membranous fold arising from the floor of the vagina fits so snugly in the genital passage as to be able to thwart attempts to inseminate queens artificially by his method or perhaps sometimes to defeat efforts to insert the glass syringe by the Watson method.

MATING STATIONS AN EARLY STEP IN THE BREEDING PROGRAM

In spite of many handicaps, the bee breeder has not been idle. During the period when he was attempting to bring the mating of the honeybee under laboratory control, he made such use of natural matings as he could by establishing mating stations in isolated bee-free localities, taking virgins and drones of desired stock there to mate. The possibility, however, that the queen may mate with a stray drone, even in a locality thought to be well isolated from local bees, reduces the value of mating stations in a scientific breeding program.

The first reported use of isolated localities in an endeavor to obtain pure matings of bees was that by Baldenstein (*2*) in Germany in 1848. Breeders in a number of European countries are now carrying out investigations by means of bee-mating stations. In Switzerland the association of German-speaking beekeepers has for a number of decades conducted a well-supported movement, inaugurated by the Swiss beekeeping leader Kramer, to maintain and improve the native Swiss bee by having selected queens mate in isolated localities at stations stocked with drones of desired strains. The mating stations are in charge of personnel from the beekeepers' association. Beekeepers bring virgin queens or queen cells in mating nuclei to these stations and take back the mated queens. The method resembles the use of community-owned sires in cattle breeding.

On this side of the Atlantic such stations have not been used so much in scientific investigations. The notable exceptions are the breeding experiments conducted a number of years ago in Texas by Newell (*21*), and those by Sladen (*34*), of Canada, in progress on an island in Lake Ontario at the time of his death in 1924. Even commercial queen rearers have made little use of mating stations, because in this country isolated locations free from wild swarms or colonies of neighboring beekeepers are not easily accessible to most queen

rearers. In Colorado, however, a strain of the Caucasian race was maintained for at least 25 years through natural matings in an isolated locality (*1, p. 40*). Certain commercial queen rearers in this country have attempted insofar as possible to duplicate conditions found in an ideal mating station by endeavoring to rid the territory in the immediate vicinity of their mating yards of undesirable colonies of bees. Their methods have consisted of buying up colonies found in the neighborhood, requeening colonies nearby with desired stock free of charge, paying rewards for wild swarms, and similar measures.

OBJECTIVES OF THE BEE BREEDER

What are the immediate objectives of the bee breeder? He may attempt to standardize the various strains now existing that are of economic importance. He may even attempt to develop strains that are more gentle, more disease-resistant, capable of carrying larger honey loads, or capable of flying longer distances than strains now available. He may attempt to develop strains with tongues long enough to secure nectar from floral sources not now available to the honeybee. For some regions it would seem desirable to develop strains that fly at lower temperatures than do bees now commonly found in the United States. This is of particular importance to those interested in bees as pollenizing agents.

The breeder need not await the occurrence of mutations, or an exhaustive survey of existing strains, to find some definite character of economic importance with which to begin work. On the contrary, he is able to start at once toward his goal, a bee better adapted to present agricultural demands, since not one but several desirable characters have already been identified among the varieties of honeybee now used in the apiary. Other desirable characters may exist, while still others are to be expected from future mutations occurring either naturally or under experimental conditions.

What are the characters in the available germ plasm with which work may be begun immediately? They are related to disease resistance, color of comb cappings, size of body parts, constancy of color markings, disposition, swarming propensity, and the like. For instance, the breeding of a bee in which are incorporated the long tongue of the Caucasian, the gentleness of the Caucasian and the Carniolan, the white capping made by the common black bee and the Carniolan, the reduced swarming tendency and resistance to common hive enemies and European foulbrood of the Italian, the uniformity of marking of the Cyprian, and the industriousness of the Italian or Cyprian would be a big achievement. Some commonly accepted worker characters, desirable and undesirable, and the races in which they are found are given below:

Character	Race
Resistance to European foulbrood	Italian.
Fighting wax moth	Italian, Cyprian.
Hive cleanliness	Italian.
Clinging to frame during manipulation	Italian, Cyprian.
Running on frame during manipulation	Common black, European brown.
White cappings on honey	Common black, European brown, Carniolan.
Water-soaked cappings	Cyprian.

Character	Race
Tongue length over 6.75 mm	Caucasian.
Tongue length under 6.25 mm	Common black, European brown.
Long legs	Caucasian.
Uniformity of markings	Cyprian.
Yellow scutellum	Do.
Gentleness	Caucasian, Carniolan.
Viciousness	Cyprian.
Reduced swarming tendency	Italian.
Excessive swarming	Common black.
Propolizing tendency	Caucasian.

BEE BREEDING IN THE UNITED STATES

Investigations of the Department of Agriculture

The Department of Agriculture was a pioneer in providing the American beekeeper with new breeding stock. It began this work by bringing in bees from Europe in an effort to have better blood than

Figure 3.—Multiple set-up devised in the Department of Agriculture for inseminating each equipped with a microsyringe and apparatus to hold the queen during the opera

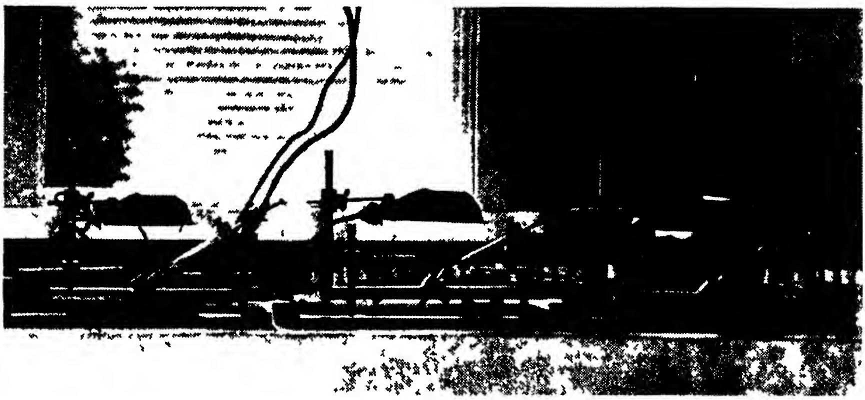
that represented by the common black bee, introduced about the middle of the seventeenth century, and as a result is credited with having established the Italian race in the United States through importations made in 1860.

In 1905 the Department sent a specialist around the world, primarily to secure the introduction of *Apis dorsata* Fab., the largest honeybee known, but the effort was unsuccessful. At that time the Department was distributing queens of the Cyprian, the Carniolan, and, more especially, the Caucasian race. During the last few years it has given further attention to a study of various races. As a result of this work and observations made by beekeepers in general, the recommendations of the Department as to an all-around bee for this country, for anyone other than the bee specialist or fancier, are usually limited to the Italian or Caucasian race.

The Department also led the way in this country in attempts to develop methods for the artificial insemination of queen bees. As early as 1885, the date when it employed its first full-time specialist

in beekeeping, it set forth as one of his duties: "To make experiments in the methods of artificial fertilization and, if possible, demonstrate the best process by which the same may be accomplished." Some slight success was reported from this early venture, and a method described in which a fine-pointed syringe was employed, as in the present Watson method, but this early work was not followed up. In 1907 the Department conducted unsuccessful attempts to obtain the mating of queens on the wing within enclosures.

Within the last few years the Department (*23*) has greatly simplified the technique and equipment for the Watson method, reducing the cost of equipment and making it possible to operate on several queens more or less simultaneously, thus increasing the output (fig. 3) Some of the special features of this new equipment differentiating it from that developed by Watson are as follows: Only one microscope is needed in using a large number of syringes; a cheap and easily made manipulator is provided for the microsyringe; the queen is held in a



several queens more or less simultaneously The set-up shown consists of 6 separate units, tion. One microscope serves the entire set-up, being moved from unit to unit as needed.

glass tube with only her abdominal tips projecting, instead of being bound by thread to a small wooden block hollowed out to fit her body; and the queen's abdominal tips are spread apart by a pair of metal hooks held mechanically instead of by forceps held by hand (fig. 4). With this equipment the genital opening of the queen can be found quickly under the miscroscope, and the microsyringe then can readily be brought into correct position for discharging the sperm without injury to the queen.

A durable microsyringe, all metal except for the minute plunger tube of glass that holds the sperm, has been developed from an automatic pencil by substituting a fine wire plunger for the lead and attaching the plunger tube to the point of the pencil. The earlier syringe consisted of a piece of glass tubing drawn out to proper shape for holding the plunger and plunger mechanism, as well as for attaching the plunger tube.

Sperm to fill the syringe is obtained by causing partial eversion of the drone organ by pressure on the drone, after which the bulb con-

taining both sperm and mucus is pulled loose with a pair of forceps. With the bulb still held in the forceps, the end containing the white mucus is cut away and the remainder, forming a minute sac containing the cream-colored sperm, is slipped over the point of the syringe. The sperm is then drawn into the plunger tube.

The Department has also modified the Quinn-Laidlaw method for artificial insemination, commonly referred to as a "hand-mating"

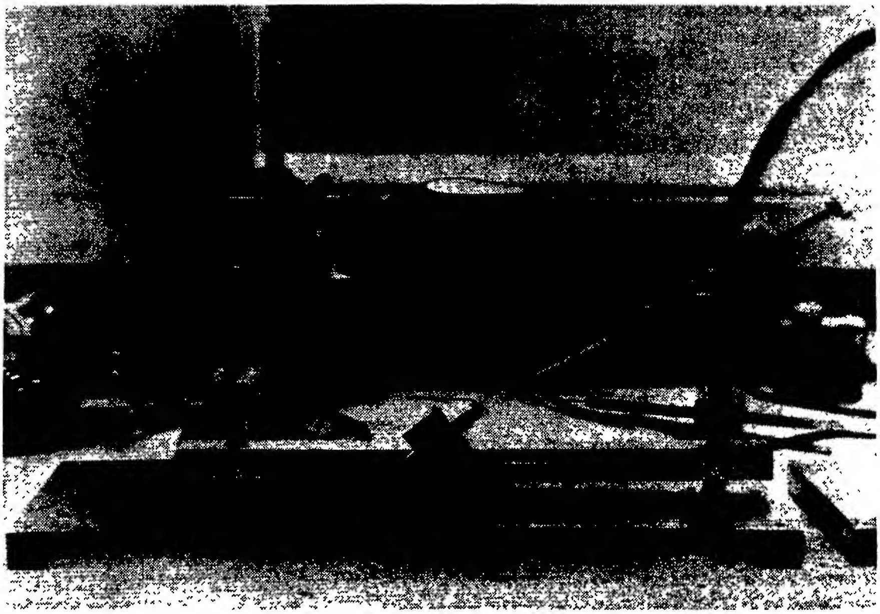


Figure 4.—Separate unit of the multiple set-up, showing queen and microsyringe in position. The microsyringe differs somewhat in construction from the original Watson type but works on the same principle. A less fragile microsyringe, all metal except for the glass point and with the movement of the plunger in and out caused by direct action, has since been devised in the Department.

method, by using a glass tube to hold the queen and a small spring placed inside her abdominal tips to hold them apart (*14*). A microscope is now used during the process. As when the method was first developed, the drone is so held by hand as to cause partial eversion of its genital organs and is then so placed in relation to the queen that the transfer of sperm will be accomplished after complete eversion has taken place.

Biometric data on common races of the honeybee and on the progeny of various crosses made by controlled matings are being collected by the Department to determine racial or strain characters of a quantitative nature and their behavior in crosses. The data collected so far consist mostly of linear measurements of various parts of the head, thorax, and abdomen. The specimens are mounted on slides under a microscope and the measurements are made on projected images (fig. 5). Those of head parts (fig. 6) include

tongue and scapus (the long joint of the antenna). On the thorax they cover counts of hooks on the hind wing and dimensions of the fore wings (fig. 7, *A*) and hind legs (fig. 8). On the abdomen the measurements deemed important are width of the third tergum (the upper surface of the third segment), longest width of third sternum (lower surface of third segment) across its left wax plate, and longest dimension of the wax plate itself. The first two abdominal segments, because of their shape and lack of wax plates, do not lend themselves to such measurements (fig. 9).

Figure 5.—Apparatus used in the Department of Agriculture for measuring external parts of bees. A micrometer eyepiece with a movable scale is attached to the microscope.

The size of the foregoing parts is of economic interest as well as of value in distinguishing races or strains, because nearly all of them function directly in the gathering of nectar and pollen and in the production of wax. The tongue, for instance, is of importance in nectar gathering. The wings are important in all activities taking the bees away from the hive. The hind legs carry pollen. The abdominal segments contain the wax plates, and may serve to limit the size of the honey sac.

Characters of a qualitative nature are also being studied. These include gentleness, industry, disease resistance, and the like. At the present time the Department is engaged in a cooperative undertaking with the States of Iowa, Texas, Wisconsin, and Wyoming, to search for stock resistant to American foulbrood, and then to combine the factor for resistance, if any be found, with other desirable factors by breeding.

During the past year the Department has employed a trained geneticist for the first time in its beekeeping work. His immediate genetical problem is to determine whether heritable factors affect supersedure, especially the premature supersedure of queens sold commercially. By "supersedure" is meant the replacement of the queen by another reared by the colony apparently for that purpose.

If heritable factors play a part in this behavior, they may lie in the behavior of the queen alone—lack of fecundity, for example—or they may lie in the behavior of the workers—for example, undue hostility to a queen reared in another colony.

State Bee-Breeding Work

Only a few States have been engaged in breeding work. A number of years ago Shafer (*30*), at the Michigan Agricultural Experiment

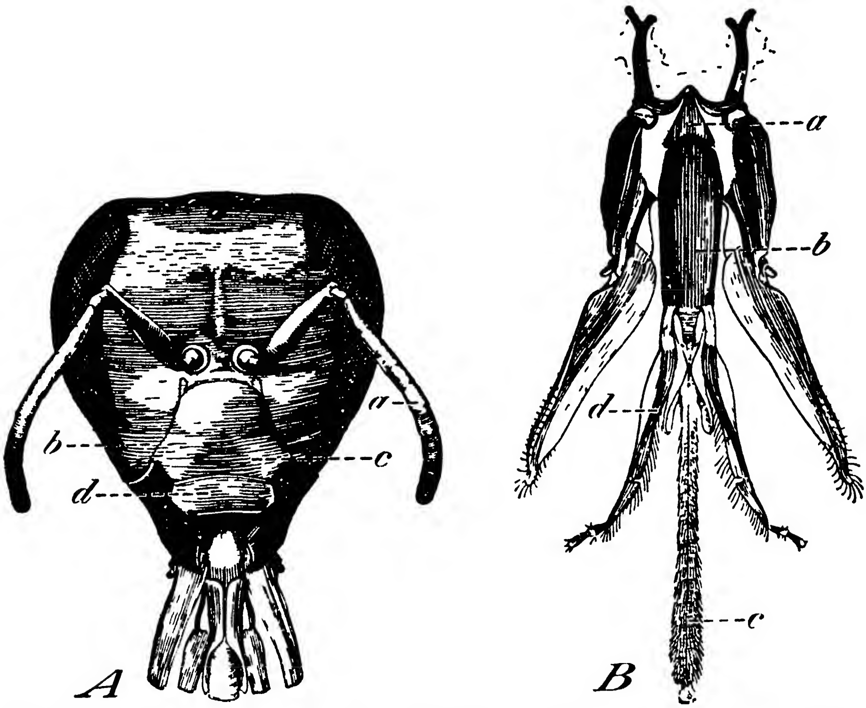


Figure 6.—*A*, Head of bee, showing: *a*, Antenna; *b*, gena; *c*, clypeus; and *d*, labrum. Tongue is shown extruded but cut off. *B*, Extended tongue, showing: *a*, Submentum; *b*, mentum; *c*, ligula; and *d*, labial palpus. (Drawing by Snodgrass.)

Station, made an unsuccessful attempt to obtain controlled matings of queen bees by natural insemination. The New Jersey Station conducted bee-breeding work in an isolated location for a number of years in connection with a study of disease resistance. More recently the Iowa Station, in cooperation with the American Bee Journal, has been engaged in a program to find stock resistant to American foulbrood and to breed for this character. The Texas Station is endeavoring to breed a bee that will better withstand Texas weather and possess greater honey-gathering ability than present strains. The College of Agriculture of the University of California is studying the correlation between physical characters of queens and their productivity, and is also studying environmental factors that influence the development of queens. The College of Agriculture of the University

of Minnesota a number of years ago conducted work on the artificial insemination of queen bees by the syringe method, with some slight success. In this work, performed by Jager and Howard (*10*), the sperm was diluted with salt solution.

Merrill (*16*), while in charge of apicultural work at the Kansas State Agricultural College, became the American pioneer in the biometric study of the activities of the colony as a whole. He attempted to correlate honey production with tongue length, size of honey sac, and other physical characters. A few years ago Munro (*19*), while a student at this college, made a study of color inheritance, using natural matings. At present E. J. McNay, a graduate student at the same institution, is making use of the Watson method in breeding work.

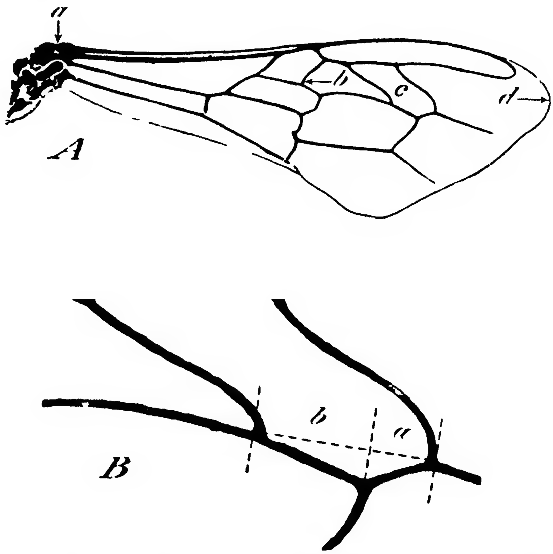


Figure 7. *A*, Front wing of honeybee, showing: *a–b*, Proximal length measured; *b–d*, distal length measured; *c*, third cubital cell. *B*, Cubital cell enlarged to show method of measuring cubital index (*a*/*b*). (Drawing by Snodgrass.)

Work by Private Breeders

The outstanding bee-breeding work of a private nature is that by Watson (*36*, *37*), who developed the method for the artificial insemination of queen bees that bears his name, and who now holds a Guggenheim fellowship for the study of bee breeding. He is making a survey of tongue lengths of various strains in an endeavor to develop a longer tongued bee than is now available. He is also trying by artificial insemination to perpetuate the "Albino" bee, a mutation of the Italian that appeared in this country about 50 years ago but has now apparently disappeared except for stock in Watson's apiary. This bee is marked by an unusually large quantity of long gray or white hairs, especially on the abdomen.

Jay A. Smith is using the Watson method in an endeavor to breed a more yellow and gentler bee. In a private communication he reports success in diluting the sperm with a saline solution before taking it into the microsyringe.

About 25 years before the present methods for the artificial insemination of queen bees were developed, Root (*26*) greatly stimulated interest in bee breeding through publicity given a "red clover queen" of the Italian race, from which was bred progeny said to have exceptionally long tongues for Italian bees. This strain soon disappeared. Among present-day workers in this country who are endeavoring to

breed bees by natural insemination may be mentioned Ralph Benton and Erwin Alfonsus, the latter formerly with the University of Wisconsin.

Balinkin (*3*) and Clifford Muth have pioneered in this country in the application of ultraviolet rays to young queens, but details of their method have not yet been published. An increase in egg laying and progeny with better dispositions were reported, but it was not claimed that this modified behavior is transmissible.

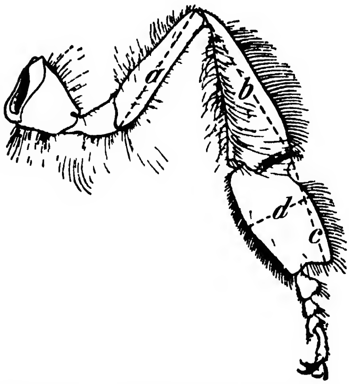


Figure 8.—Hind leg of worker bee, showing measurements made: *a*, Length of femur; *b*, length of tibia; *c*, length of metatarsus; *d*, width of metatarsus. (Drawing by Snodgrass.)

BEE BREEDING IN FOREIGN COUNTRIES

Numerous foreign workers are interested in bee breeding (see the appendix). The work of the German-speaking beekeepers' association in Switzerland has already been mentioned. Breeding along the same lines is in progress in Germany and elsewhere in central Europe. Zander (*40, p. 193*), assisted by A. Himmer, for years used isolated mating stations to breed an improved strain of the European brown bee, as part of the program of the bee-research institute at Erlangen. Armbruster (*2*) is another German investigator who has worked in this field.

Gotze (*7*), also of Germany, has been engaged in a biometric study of progeny of crosses obtained at mating stations. He has reported unsatisfactory results in the use of artificial insemination. He places considerable reliance upon certain indices, which are based on proportions involving certain wing cells, as a means of identifying various strains with which he works. The most important of these is the cubital index, which is the ratio of the two parts into which the line joining the two corners of the third cubital cell of the front wing on the side bounded by the cubital vein is divided when a perpendicular is dropped from this line to the second recurrent vein (fig. 7, *B*, illustrates this measurement).

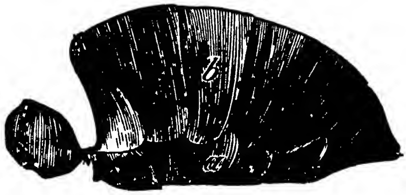


Figure 9.—Lateral view of worker abdomen showing the six abdominal segments, including a portion of the thorax at left: *a*, Left end of third abdominal sternum; *b*, left end of third abdominal tergum. (Drawing by Snodgrass.)

Alpatov (*1, p. 24*), of the Union of Soviet Socialist Republics, has perhaps made a wider use of biometrical indices in studying the differences of races or strains than has any other investigator. Some indices used by him are the proportion between width of the first wax gland and width of the sternum that contains it, length of the hind metatarsus and width of third abdominal tergum, length of hind tibia and width of third abdominal tergum, length of hind femur and width of third abdominal tergum,

distal length and proximal length of front wing, and width and proximal length of front wing (figs. 7, 8, and 9).

Jaroslav Rytiř, of Czechoslovakia, has made observations on the inheritance of measurable characters of various strains, including "strain 47". This strain was developed, or rather perpetuated, by the Austrian queen breeder Sklenar (*31, p. 5*) from a colony that had been outstanding in his apiary. Sklenar thinks the strain is descended from a mixture of the Carniolan and Italian races, although the workers show no yellow color. They are usually gray but occasionally one is reddish brown. Rytiř (*27*) has also studied inheritance of amount of coloration on abdominal segments, and has devised a workable system for obtaining quantitative data on this characteristic.

A few years ago Mikhailoff, of the Union of Soviet Socialist Republics, reported considerable success with the Watson method. From the same country also came the Malyschev method (*15*). This differs from the Quinn-Laidlaw method in that the drone organ is first dissected out under the microscope and then placed in position in the queen. Prell (*25*), of Germany, working independently, reported success with a method like that of Malyschev.

GEOGRAPHICAL STATUS OF DEVELOPMENT OF BREEDING TECHNIQUE

In the United States successful methods for the controlled mating of queen and drone under laboratory conditions have been developed and existing races of the honeybee have been tried out. In western and central Europe workers have made praiseworthy attempts at the improvement of bees by selective breeding in isolated mating stations. In the Union of Soviet Socialist Republics breeding work has centered largely around biometric studies in an endeavor to reduce the characteristics of races and strains to some sort of mathematical formula whereby each can be more easily distinguished. Some work has been carried out with artificial insemination.

CYTOLOGICAL STUDIES [2]

Too little is known concerning the cytology of the honeybee. For a long time the work of Nachtsheim (*20*), which seemed to show that the diploid number of chromosomes (that of queen and worker) is 32 and that the haploid number (that of drones) is 16, has been accepted as standard. In recent work, however, Sanderson (*29*) has questioned whether Nachtsheim has reported the normal numbers or whether they are not 16 and 8 for queen and drone, respectively. The characteristic shape of any of the chromosomes has not yet been determined.

Even the type of sex chromosome and the method of sex determination in the honeybee are still undetermined. Nachtsheim holds that the sex chromosomes are of the X type, the female possessing two and the male but one, since the drone arises from an unfertilized egg. Likewise the female possesses twice as many other chromosomes (autosomes) as does the male. Consequently, according to Nachtsheim, sex is determined on a quantitative basis—doubling the sex

[2] The following sections are written primarily for students and others professionally interested in breeding or genetics, although some of the results discussed are also of general interest

chromosome and autosome complement results in a female instead of a male. This view is not in accord with the theory of genic balance that is now applied to so many organisms. According to this theory, sex is not determined on a quantitative basis, but is the resultant of a tendency towards maleness or femaleness in genes of the autosomes taken as a group and an opposing tendency in genes of the sex chromosomes.

In contrast to Nachtsheim's theory of sex chromosomes in the honeybee, Whiting (*39*) holds that in the parasitic wasp *Habrobracon juglandis* Ashmead, another hymenopterous form in which males develop parthenogenetically, the two sex chromosomes of the female are of the XY and not of the XX type. Consequently two types of haploid males develop, depending on whether they contain a single X or a single Y chromosome. Outwardly they appear alike, but they can be identified genetically. They are produced in equal numbers. Of even greater interest, two types of biparental males are to be found and these contain either two X or two Y chromosomes. Biparental males, like the females, carry two sets of autosomes, but cannot be distinguished from the ordinary parthenogenetic males unless the parent male possesses a factor that is dominant to the homologous factor carried by the homozygous mother.

Whiting (*39*), basing his conclusions on experimental evidence, explains sex determination in *Habrobracon* by assuming that the X chromosome carries the factors $F.g$ while the allelomorphs ($f.G$) of these two factors are carried by the Y chromosome. The presence of both F and G, classed as "complementary factors" by Whiting, is necessary for the development of a female, otherwise only a male will result. The dominants F and G would both be present, of course, whenever fertilization of the egg represents the union of X and Y, since the egg would then carry the factors $F.g/f.G$. The union of a sperm and an egg each of which has an X chromosome, or each of which has a Y chromosome, could only result in a biparental male, because in either event the fertilized egg would contain only one of the two dominant complementary factors necessary if a female is to result. The factors in the one case would be $F.g/F.g$, and, in the other $f.G/f.G$. Whiting's line of reasoning would hold, whether F and G each represents only a single dominant gene or whether they are the symbols of a group of dominant genes carried in their respective chromosomes (X and Y).

Whiting (*38*) first encountered biparental *Habrobracon* males in a culture headed by a female homozygous for orange-colored eyes but mated to a male with black eyes, the dominant color. Instead of all the sons having orange eyes, a few resembled the daughters in having black eyes. Such males usually proved sterile, although in certain instances in which they were mated with females homozygous for orange-colored eyes a few daughters were obtained, some with orange eyes and some with black eyes. A knowledge of whether or not Whiting's results on *Habrobracon* hold good for the honeybee awaits further work.

The fact that the drone is haploid seems to have led to the impression that drones from a heterozygous queen will be only of two kinds,

corresponding to the queen's maternal and paternal inheritance. Such a conclusion holds only if one pair of unit factors or linkage groups is under consideration. For example, normally half the drones from a queen heterozygous for color say, yellow and black—would carry the factor for yellow and half of them the factor for black if these were unit factors. Her drones would fall into four types, however, if their inheritance of any two pairs of unlinked factors is considered. Thus, if it is assumed that the characters for tongue length and those for color are not linked, but that each is determined merely by a unit factor, a queen heterozygous for these two factors would produce long-tongued yellow drones, short-tongued yellow drones, long-tongued black drones, and short-tongued black drones. The greater the number of pairs of unlinked factors that are under consideration, the greater will be the number of types into which the drones can be classified.

RESULTS OBTAINED FROM BEE BREEDING

It is unfortunate that Mendel's detailed records have never been brought to light. His studies were not confined to one race of the honeybee, since it is reported (*9*) that he worked on the heather or Dutch bee, the Italian, the Carniolan, the Egyptian, and the Cyprian, in addition to the native bee of his region.

Since so much of the work concerned the development of a technique for breeding the honeybee under controlled conditions, and a biometric study to determine measurable physical characters of individual members of a colony as well as characteristic colony behavior marking races or strains, strictly genetic results are scanty as yet, and often of a somewhat general nature.

The work of the Department has verified the fact that honeybees can be successfully carried from generation to generation by means of artificial insemination, seven successive generations having been obtained in three seasons' work. Allowing the queen 16 days to develop from egg to adult, 7 days in which to mate, and 3 more in which to begin egg laying, there should theoretically be a laying queen of each successive generation every 26 days, but the normal hazards and delays of beekeeping have greatly increased this period in actual practice.

The Department has verified Watson's feat (*37*) of transferring sperm from the spermatheca of one queen to that of another. The queen from which sperm was transferred had been dead for several hours. This procedure makes possible a type of line breeding, involving crosses of a drone with his offspring, although on an extremely limited scale, because the supply of sperm from the original drone cannot be replenished but will be diminished when transferred from queen to queen.

The work of the Department also indicates that color and tongue length can be inherited independently of each other and that each race has its own size characteristics, which are inheritable and more or less constant within fairly definite limits. Judging from preliminary data, some correlation exists between tongue length and number of wing hooks, and also between tongue length and length of scapus. Götze's statement (*7, p. 227*) of the correlation between tongue

length and length of labial palpi also seems borne out by the work thus far.

A hitherto undescribed mutation, involving a yellow coloration on the face of the bee—principally on the clypeus, genae, labrum, and, at times, bases of antennae (fig. 6, *A*)—was found in an Italian strain in the Department's apiary formerly at Somerset, Md., and an attempt is being made to obtain a homozygous strain. However, it appears to be a recessive character.

The development of stock especially resistant to European foulbrood was announced as the result of selective breeding experiments in New Jersey (*6*). In describing the first season's work of the Iowa Agricultural Experiment Station to find stock resistant to American foulbrood, Park (*24*) concluded that variation in resistance to American foulbrood exists. Some evidence of the inheritance of number of egg tubules has been reported in a private communication from J. E. Eckert, describing work at the University of California.

Since the World War an independent breeder, Henry Brown of New Jersey, has developed a light-colored strain, reputed to be very gentle, by crossing the Cyprian and Italian races, according to a private communication.

Even years before Brown's work the "golden" Italian bee, a strain with the anterior portion of each of the first five abdominal tergites marked with a golden band, instead of only each of the first three as in the ordinary Italian, was developed in this country, supposedly by crossing the Italian with the Cyprian. This golden Italian, while held to be gentle and a beautiful bee, had little repute as a honey gatherer. Sladen (*32*) developed a "British golden" by crossing the English strain of the common black bee, the Italian, and the "American golden." By continued selective breeding in an isolated locality, a bee was obtained which Sladen claimed combined the hardiness and industriousness of the black with the prolificness of the Italian, although its area of golden coloration was not so extensive as that of the "American golden." No attempt was made to increase the area of golden coloration, however, since this character was used merely to provide breeding stock with drones of such a color that their progeny could easily be distinguished from that of the common black drone, which prevailed elsewhere in the locality.

Jay A. Smith reports in a private communication that in crosses obtained by the Watson method no correlation seemed to exist between color and gentleness.

The reports of the work in Switzerland are of especial interest to beekeepers, since rather extensive records are kept showing the returns from improved (veredelte) stock, meaning that developed at the mating stations, as compared with those from ordinary or unimproved stock. Thus from 1915 to 1928, according to a survey of certain apiaries which contained colonies of both types of stock, the honey crop of the improved stock averaged larger per colony each year than that of the unimproved stock, ranging from 20 percent more in 1923 to 100 percent more in 1924 (*13, p. 30*).

Mikhailoff (*18*) used the Watson method of insemination to demonstrate that the spermatozoa from white-eyed drones are active,

and he succeeded in obtaining white-eyed workers and queens. White-eyed drones apparently do not see and do not mate in nature. That the gene for white eyes is recessive to the normal eye color is shown by the fact that with natural mating a queen laying eggs from which white-eyed drones arise gives only workers with normal eye color.

In the Department apiary formerly at Somerset, Md., half of the drones from an Italian queen that produced white-eyed drones were white-eyed and half were black-eyed, a proportion also observed by other investigators. A few of the white-eyed drones were seen to fly off into the air, but none was seen to reenter the hive. Some, on leaving the hives, made short hops or flew in small circles away from the hive entrance. In the fall only black-eyed drones were found in the hive with this queen. Whether at this season the workers removed the white-eyed drones before emergence is problematical, since no white-eyed drone pupae were found in any of the sealed cells. A number of virgins were reared from this queen, but attempts to inseminate them with sperm from the white-eyed drones were unsuccessful. One of these virgins inseminated with sperm from a normal drone, however, produced some white-eyed drones. Part of the worker progeny of the original queen were a lighter yellow on their abdomens than the ordinary Italian bee.

As for the inheritance of quantitative characters, Mikhailoff reported (*17*) that a Caucasian queen from a colony with a tongue length of 6.9393 mm was mated with a central-Russian black bee with a tongue length of 6.1729 mm, and the resulting cross gave a bee with tongue length of 6.705 mm. Twelve percent of these hybrids had tongue lengths of 7.0282 mm, this being greater than that of either parent race. Two Caucasian queens that were inbred with "brother" drones had progeny with shorter tongues than those of their worker sisters. Other quantitative data are included and, although they represent a very scanty number of colonies, they are of interest because they are the first statistical data to be published that are derived from controlled crossing of the honeybee.

Alpatov (*1*) has concludedas a result of his studies in the Union of Soviet Socialist Republics that, in the area covered, absolute size of body and of wings, relative size of the wax gland, and the color of the abdomen seem linked. The same is true concerning length of tongue and length of hind legs. He (*1, p. 40*) has pointed out that the constancy of color of the yellow and the black races in the United States shows that color is an inherited racial characteristic.

Watson (*37*) has stated that the albino bee is dominant over the common black bee.

Newell (*21*) crossed yellow Italians and black Carniolans and found yellow dominant. Watson (*37*) crossed a black virgin and a yellow drone and obtained all black offspring. It may be assumed that Watson used the common black or Dutch bee. Sladen (*33, p. 64*), in crossing a golden queen with pure black drones, obtained "intermediate" workers that had black bands on the posterior margins of the second to fifth abdominal tergites, increasing in width from tergite to tergite toward the rear. The sixth tergite was black As a matter of fact, the last abdominal tergite is black in all varieties of

the European honeybee, no mutation showing a different color having yet been reported.

In work at the Department (*22*) a daughter of a European brown bee crossed with a yellow drone produced workers that might have been taken casually as a dark strain of three-banded Italians, possibly because of the blackness of the posterior bands of each of the first three abdominal tergites. Practically the same results were obtained later with Caucasians and Italians.

Mikhailoff (*17*), in crossing queens of the central-Russian black bee with golden Italian drones, found yellow to be the dominant color in 90 percent of the progeny.

Götze (*8*) holds that the yellow scutellum, such as occurs in the Cyprian and other eastern races, is the expression of a dominant unit factor. He found that a golden queen mated to a black drone gave workers with yellow scutella. These workers, however, as regards abdominal coloration, were not golden, but had abdominal segments with decided black edges, as in the work by Sladen and the writer. Götze (*8, p. 71*) therefore calls the F_1 an "intermediate form" and further assumes that a separate gene is responsible for the black edges on the abdominal segments.

Götze has found in various colonies both black and brown drones as well as some termed by him "leather-colored." To account for these various colorations he assumes a basic color factor, *N*, which requires the presence of an activating factor to give rise to color. He assumes that not one but two activating factors or their allelomorphs are carried. These are *M*, a factor for black, and *B*, a factor for brown. *B* is inhibited by *M*. When only their allelomorphs *bm* are present, leather-colored individuals arise. Gotze states that *m* is a factor for leather-colored but does not give the nature of *b*. A black drone, according to this scheme, would have the genic composition *NBM* or *NbM;* a brown drone, *NBm;* and a leather-colored drone, *Nbm*. In addition, Götze found that certain eggs did not hatch, and he holds that they had the genic combination *nbm*, which he assumes is lethal. In an actual count, omitting the supposed lethal cases, he found 110 black, 48 brown, and 21 leather-colored workers.

Stucki (*35*) has suggested the possibility that certain definite excesses or deficiencies from the normal wing venation may be characteristic of certain strains of Swiss bees, although he postpones definite conclusions until more material is accumulated. Like Casteel and Phillips (*5*) and others, he found drones especially variable. Rytiř (*28*) reports, as a result of crossing the Iskra strain of bees from Czechoslovakia with the Nigra strain of the European brown bee—the latter strain having a lower cubital index (fig. 7, *B*)—that the lower index is completely dominant over the higher.

The dominance or recessiveness of certain characters of the honeybee that have been reported as heritable is shown below. It is to be remembered that most of the data need further confirmation before being accepted and that, while many of the characters listed seemingly have little or no direct economic importance in themselves, yet, if they happen to be linked with characters of economic importance, perhaps they may ultimately prove of use as an index to the presence of such characters.

Dominance or recessiveness as shown in F_1 generation

Dominant factors	Recessive factors	Reported by—
Eye color normal	Eye color white	Mikhailoff (*18*).
Abdominal marking:	Abdominal marking:	
Italian	European brown	Mikhailoff (*17*).
Do	Carniolan	Newell (*21*).
Common black	Italian	Watson (*37*, *p. 40*).
Albino	Common black	Do.
Cubital index low	Cubital index high	Rytiř (*27*).
Scutellum yellow	Scutellum black	Munro (*19*).
Clypeus, genae, and labrum dark	Clypeus, genae, and labrum yellow.	Nolan (this article, *p. 1534*).
Use of wax for sealing crevices, etc. (Carniolan).	Use of propolis for sealing crevices, etc.	Newell (*21*).

Some crosses in which dominance or recessiveness is not shown for certain characters by F_1 generation

Cross	Character	Reported by—
European brown × Golden	Abdominal coloration	Götze (*8*, *p. 71*).
Common black × Golden	do	Sladen (*33*, *p. 64*).
European brown × Italian	do	Nolan (*22*).
Long × short	Tongue length	Götze (*8*, *p. 73*).

Some linked characters

Characters	Reported by—
Absolute size of body and wings, relative size of wax glands, color of abdomen.	Alpatov (*1*, *p. 48*).
Tongue length, labial palpi	Götze (*8*, *p. 227*).
Tongue length, number of egg tubules	Komarov and Alpatov (*11*).
Yellow color, light weight (drones)	Munro (*19*).
Black color, heavy weight (drones)	Do.

Now that a notable advance in the technique of accomplishing matings has been made, methods for obtaining biometric data have been worked out, and germ plasm that possesses a number of desirable characters is available, the way appears open for a worth-while advance in bee breeding, although quick results should not be expected.

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APPENDIX

Some Workers Identified with Bee Improvement at State and Federal Experiment Stations and Other Institutions

State Agricultural Experiment Stations:
- California, Davis: J. E. Eckert.
- Connecticut, New Haven: L. C. Curtis.
- Iowa, Ames: O. W. Park.
- Kansas, Manhattan: E. J. McNay.
- New Jersey, New Brunswick: R. S. Filmer.
- Texas, San Antonio: H. B. Parks.
- Wisconsin, Madison: H. Laidlaw.

Other institutions:
- Brigham Young University, Provo, Utah: J. Fleming Wakefield.
- Alfred University, Alfred, N. Y.: L. R. Watson.
- Depauw University, Greencastle, Ind.: Jay A. Smith.

United States Department of Agriculture, Bureau of Entomology and Plant Quarantine:
- Baton Rouge, La.: Otto Mackensen.
- Beltsville, Md.: W. J. Nolan.
- Laramie, Wyo.: A. P. Sturtevant.

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Some Workers in Foreign Countries Identified with Bee Improvement

Austria, Mistelbach: Guido Sklenar.
China, Fukien Christian University, Foochow: C. R. Kellogg.
Canada, Dominion Experimental Farms, Ottawa: C. B. Gooderham.
Czechoslovakia, Krpy: Jaroslav Rytiř.
Czechoslovakia, Ober-Hohenelbe: Egon Rotter.
Egypt, Matarich, Cairo: A. Z. Abushady.
Germany, Landesanstalt für Bienenzucht, Erlangen: E. Zander and A. Himmer.
Germany, Landwirtschaftliche Hochschule, Hohenheim bei Stuttgart: G. A. Rösch.
Germany, Rheinische Lehr- und Versuchsanstalt für Bienenzucht, Mayen-Eifel: G. Götze.
Germany, Berlin-Zehlendorf: L. Armbruster.
India, Punjab Agricultural College, Lyallpur: S. Singh.
Italy, Instituto Zoologico della R. Università di Bologna: Anita Vecchi.
Switzerland, Verein Deutsch-Schweizerischer Bienenfreunde, St. Gallen: M. Jüstrich.
Union of Soviet Socialist Republics, Ecological Laboratory, Moscow: W. W. Alpatov.
Union of Soviet Socialist Republics, Petrovka, Moscow: A. S. Michailoff.

FUNDAMENTALS OF HEREDITY FOR BREEDERS

E. N. BRESSMAN, Scientific
Adviser, Office of the Secretary [1]

THE preliminary articles in the 1936 Yearbook included some discussion of the fundamental nature of genes and chromosomes, but very little about how the chromosomes, the carriers of the genes that are the determiners of hereditary traits, are distributed among the descendants of two parents used as breeding stock. This distribution occurs in certain genetic ratios, which were first discovered by Johann Gregor Mendel and gave the clue to the orderly operation of heredity. Before explaining them, it is necessary to consider what happens when two reproductive cells unite to produce progeny.

WHAT HAPPENS WHEN THE CELLS UNITE

THIS has been well described by A. H. R. Buller in his account of the discovery of Marquis wheat. Buller not only understood the facts of his science of botany; he had a feeling for its poetry as well. The following description is taken from his book. Telling how all Marquis wheat plants came originally from a single kernel or seed, the offspring of a cross between Red Fife and Hard Red Calcutta selected by the famous Canadian plant breeder, Charles Saunders, Buller wrote: [2]

> Pollen dust from some stamens removed with forceps from a few flowers of [Red Fife] was placed on the two feathery stigmas of a flower of [Hard Red Calcutta]. The pollen grains germinated, each grain producing a single pollen tube. The pollen tubes, which were exceedingly delicate cylindrical structures, grew down the stigmas and made their way, by elongating at their apices, into the ovary below. This ovary was a tiny chamber containing a single ovule or potential seed attached laterally to its wall. One of the pollen tubes, guided by chemotropic stimuli, directed its course toward the ovule, entered at its mouth or micropyle, and penetrated into its interior as far as the ovum or egg-cell. The egg-cell having been reached, the wall at the tip of the pollen tube liquefied and broke down, and from the opening so produced there were emitted two exceedingly minute dense rounded masses of gelatinous protoplasm known as male nuclei. One of these nuclei, carried by forces as yet not perfectly understood, advanced through the general protoplasm of the egg-cell toward the female nucleus situated in its center. The male and female nuclei, after coming into contact, brought their affinity for one another to a climax by mingling together and forming one whole; and this nuclear fusion, this formation of a single nucleus from two others of opposite sex, marked the completion of the act of fertilization. * * * With-

[1] Many workers in the Department have made contributions to this article. The writer is indebted particularly to George Haines, senior animal husbandman, Office of Experiment Stations, and W. V Lambert, senior animal husbandman, Bureau of Animal Industry, who have been very generous with suggestions and help on animal genetics, not only in this article but elsewhere in the Yearbook.

[2] R. Buller, A. H. ESSAYS ON WHEAT, INCLUDING THE DISCOVERY AND INTRODUCTION OF MARQUIS WHEAT, THE EARLY HISTORY OF WHEAT-GROWING IN MANITOBA, WHEAT IN WESTERN CANADA, THE ORIGIN OF RED BOBS AND KITCHENER, AND THE WILD WHEAT OF PALESTINE. 339 pp., illus. New York. 1919. See pp. 219–220.

out fertilization, the egg-cell would have * * * withered and died; but, its fertilization having been accomplished, a most extraordinary future was opened to it. Further development became irresistible, with the result that, in the course of a few years, its products became in numbers like the stars on a clear night, or the grains of yellow sand upon a sea beach.

To round out the description, it is necessary to add that when the male and female nuclei fuse, the resulting single nucleus becomes the embryo of a new plant. But this embryo is not the whole seed. It will be noted that there were two male nuclei, only one of which united with the female nucleus. But there was also more than one female nucleus, for this one was attended by two much smaller bodies known as the polar nuclei. During fertilization, these two polar nuclei united with the other male nucleus and from this separate union came the endosperm, the starchy part of the seed, the function of which is to furnish food for the embryonic plant during the initial stages of its growth. This union of a male nucleus with two female polar nuclei is peculiar to plants, and it accounts for the fact that the male parent may immediately impress certain characters on the endosperm and embryo of the seed—a phenomenon known as xenia. Except for xenia and metaxenia, the inheritance from the male parent does not appear until the new plant has grown and produced seed in its turn.

This immediate effect of the two polar nuclei, visible in the endosperm, is commonly seen in corn. When a pollen grain from purple corn pure for this characteristic fertilizes an egg cell of white corn, for example, the resulting seed is purple. In some other seeds, like wheat, the effect of xenia is not evident because the endosperm is covered with female tissue known as the pericarp; but even though it is not always observed, xenia occurs in all seed plants. It might be added here that certain other tissues associated with the seed may sometimes be affected in a similar manner by the male parent. This happens in the case of date fruits, and the phenomenon, which has been called metaxenia, is discussed in the date section of the article on subtropical fruits.

The details of the process of fertilization in animals differs somewhat from that in plants although the end result in each case is a new individual which received half of its heredity from the male parent and half from the female parent. In animals the male reproductive cells, known as spermatozoa, are produced literally by the millions in the testes or sex glands of the male. They are microscopic, motile cells, which are propelled by long hairlike tails. The larger part of the head of the spermatozoon is composed of the nucleus, the part of the cell that carries the hereditary factors. The female reproductive cells, known as ova, are produced in the ovaries or sex glands of the female. They are much larger than the male reproductive cells and are nonmotile.[3] They contain a microscopic nucleus that corresponds in size to the nucleus of the spermatozoon. The remainder of the egg consists largely of food material intended to nourish the young embryo until food connections are established with the tissues of the mother, or in the case of birds and other forms in which development takes

[3] The yolk of the hen's egg is the true egg, the remainder of the contents within the shell are secreted by the glands of the oviduct or "egg bag." Most of the yolk consists of food material. The eggs of mammals are much smaller than the eggs of birds. Most mammalian eggs are of a size that makes them barely visible to the naked eye.

place outside of the body of the female, food to nourish the embryo throughout its entire development.

In contrast with plants, the spermatozoon, which corresponds to a pollen grain, and the egg cell, which corresponds to the ovule of the plant, are ready to function in fertilization without further nuclear divisions. The sperm cells are deposited by the millions in the reproductive tract of the female at the time of mating. From the point of deposit they move in a swarm to the innermost part of the reproductive tract (the fallopian tubes) of the female, where they are ready to unite with the egg or eggs as soon as they are freed from the ovary. Normally only one spermatozoon enters the egg and takes part in fertilization although thousands of spermatozoa surround an egg. When the spermatozoon enters the egg its nucleus unites with the nucleus of the egg, and this joining of the two nuclei into a single new nucleus is what is known as fertilization. The new nucleus, which received half of its heredity (genes) from the male parent and half from the female parent, constitutes a new individual. All animals and plants begin their life as such single cells. From that point growth proceeds by a continual process of cell division and as it proceeds the new cells are formed into the tissues and organs of the body of the new animal. The processes of growth are similar in both plants and animals. The embryo observed in the seed of plants is a partially developed plant since it contains many cells that arose by the division of the fertilized ovule.

Now we must consider another aspect of those male and female nuclei whose union was described by Buller for wheat plants.

It is generally recognized that the chromosome number for a given species is constant. For example, every nucleus in each body cell of the Red Fife and Hard Red Calcutta parents contained 21 pairs of chromosomes, or 42 altogether. But the nucleus of each reproductive cell—as distinguished from the body cell—contained only 21 chromosomes, not 21 pairs. (This reduction in number occurs when reproductive cells are formed, as described by Kempton.)[4] These 21 chromosomes in the male Red Fife reproductive nucleus contained a complete set of genes capable of reproducing all the Red Fife characteristics; and the same thing was true for the female Hard Red Calcutta nucleus. The two joined, promptly lost their individual identity, and formed a new nucleus with 42 chromosomes containing all the genes of both parents, and therefore capable of producing their characteristics. From that cell came a new plant, the first-generation or F_1 hybrid[5] between the two.

Under ordinary circumstances, if the two parents are pure, all the F_1 or first-generation plants of the cross are exactly alike, for each individual offspring contains a full set of genes from the mother and a full set from the father and it expresses the dominant characteristics of both of them. Very often also these F_1 hybrid plants are unusually vigorous in size or productiveness or other characteristics, especially if the parents were considerably unlike one another. This is the well known "hybrid vigor" or heterosis, for which several explanations have been suggested.

[4] KEMPTON, J. H. HEREDITY UNDER THE MICROSCOPE. U. S. Dept. Agr. Yearbook 1936: 165–182, illus. 1936.

[5] F_1 is pronounced eff-one. The F stands for filium or filial, depending upon whether it is used as a noun or an adjective, and the subscript numerals indicate which generation is meant—first, second, third, etc.

One of these explanations is that all the dominant genes from both parents have a chance to express themslves in the hybrids. To take an imaginary example, suppose one parent had a dominant gene for height so that it was tall, but it had small leaves because of a recessive gene. Suppose the other parent had large leaves because of a dominant gene, but that a recessive gene for dwarfness made it a short plant. The F_1 hybrid would then be tall because of the dominant gene for height inherited from one parent, and it would have large leaves because of the dominant gene for leaf size inherited from the other parent. A number of such dominant genes might express themselves and in combination make the F_1 hybrid seem unusually vigorous. Or, to consider another characteristic such as disease resistance—each parent might have certain dominant genes that increase resistance. When all of these genes came together in the progeny, it might be more disease-resistant than either of the parents.

Another suggested explanation of hybrid vigor is that it is the result of physiological stimulation, which somehow comes from the mixing of unlike protoplasm from the egg and the sperm.

SEGREGATION OF CHARACTERISTICS IN THE PROGENY

But hybrid vigor is not the immediate point of this discussion. We are not concerned here with what happens in the first hybrid generation, but with what occurs in the second generation, which breeders call the F_2. This is well illustrated in figure 1.

We shall assume that both the original parents have been bred pure, and that the F_1 generation is then inbred or fertilized by its own pollen to produce the F_2 generation- the grandchildren of the original parents. What happens to the chromosomes in the F_2 progeny?

Perhaps this can best be visualized for the present by concentrating on a single pair of genes, let us say a pair governing height. Now genes have alternative forms, called allelomorphs or alleles (allelomorph comes from two Greek words meaning "alternative form"). Suppose that a gene for height in the original male parent was one that made the plant tall. Suppose that the gene in exactly the same place on the corresponding or homologous chromosome in the original female parent was an allel or alternate that made the plant short. The F_1 hybrid would receive both chromosomes, making a pair, with the gene for tallness in one and the gene for shortness in the other. These two genes would be present in every body cell of the F_1. But the time would come when reproductive cells were formed, and this would involve the separation of the two members of a pair of chromosomes, since each reproductive cell receives only one chromosome where there were two in the body cell. Thus whenever an original cell divided to form two male reproductive cells, one of them would be bound to receive the chromosome containing the gene for tallness and the other would be certain to receive the chromosome containing the gene for shortness. If several thousand male reproductive cells were produced by the plant, half of them would have the tallness gene, half the shortness gene. And the same thing would be true of the female reproductive cells.

Next this plant is to be self-fertilized; its own male nuclei are to join with its own eggs to form the primary cells of F_2 plants, the next generation. Obviously there could be four kinds of these new cells.

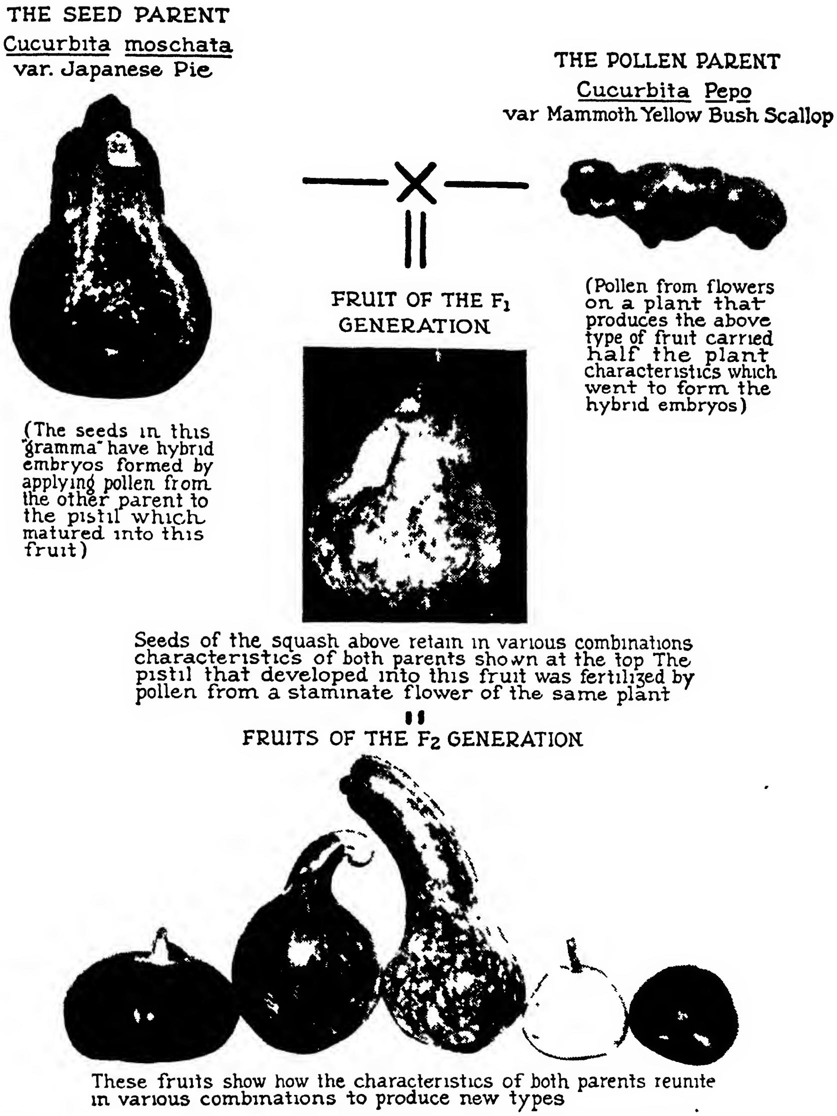

Figure 1.—**A cross between two species of cucurbits widely differing in appearance. Typical fruits of the parental types; the first generation, which exhibits dominant characteristics; and the second generation, which exhibits characteristics of both parents in various combinations. This is a typical example of the operation of Mendelism. (Courtesy of New York (State) Agricultural Experiment Station.)**

(1) A male nucleus with a tallness gene might join a female cell with a tallness gene, giving "tallness-tallness."

(2) A male nucleus with a tallness gene might join a female cell with a shortness gene, giving "tallness-shortness."

(3) A male nucleus with a shortness gene might join a female cell with a tallness gene, giving "shortness-tallness."

(4) A male nucleus with a shortness gene might join a female cell with a shortness gene, giving "shortness-shortness."

Since there are as many reproductive cells that carry the tallness gene as there are reproductive cells that carry the shortness gene and fertilization of the two kinds of eggs by the two kinds of pollen grains occurs entirely by chance, there would be equal numbers of these four different kinds of new cells if large numbers were produced. But group (2) and group (3) above would be exactly the same in effect, since each is a tall-short combination. Thus the proportions in the total population would be 1 tall-tall to 2 tall-short to 1 short-short. This is a simple Mendelian characteristic, the probable breeding behavior of which is expressed as a 1 to 2 to 1 or 1:2:1 ratio.

Thus the plants in the F_2 generation are not at all like those in the F_1. In the F_1, all are alike; in the F_2, with exactly the same basic characteristics, there are three different kinds of plants, with respect to this pair of genes, and they occur in definite proportions. That is, they occur in definite proportions if the population is large enough and is considered as a whole. If only a few plants were produced, these proportions might not hold; out of any four individuals selected at random, there would obviously be a very small chance that one would be a tall-tall, two tall-short, and one short-short. But for large numbers, the ratios hold well. This might be compared to the fact that any given family may have more boys than girls, or vice versa, but that on the whole the male and female population is about equal.

Segregation Ratios

This splitting up into several combinations of characteristics in the second generation is what is technically called segregation, and the generation in which it occurs is often called the segregating generation. Segregation occurs even in pollen grains as is shown in figure 2. It should be noted that segregation may occur in the F_1 if the parents are hybrids rather than bred pure. For example, if the hybrids in this example were the original parents, segregation would begin in the first generation after they were selfed or crossed. But this would be merely a change in names; what was really the F_2 would now be called the F_1. It is important to remember, however, that whenever hybrid material is used to start with—as it often is in practice—segregation is apparent in the first generation. In fact, this is the test that proves whether the parent material is hybrid or pure. If a breeder takes a plant the ancestry of which he does not know, selfs it, and finds the progeny in the next generation segregating into different types, he knows the original plant must have been a hybrid. This is what happens, for example, with ordinary open-pollinated varieties of corn. Upon being selfed, the progeny begins to segregate into types immediately.

Before going on with the discussion of segregation ratios, it might be well to consider what happens on further inbreeding of these F_2 plants. We derived three kinds—the tall–tall, the tall–short, and the short–short. When reproductive cells are formed in the tall–tall plant, obviously every one of them must receive a tallness gene, since there is no other. Thus when such plants are selfed all the descend-

ants of the tall–tall plants will also have the tall–tall combination, and this will go on indefinitely as long as they are selfed. Likewise, the short–short plants will produce only short progeny. Whenever an organism has exactly the same genes for a certain character on both members of a pair of homologous chromosomes, it is said to be homozygous for that character Ordinarily, it will go on breeding true for that character indefinitely as long as it is selfed. From a genetic standpoint, this is what pure breeding means. Often the effort of the plant breeder is to produce plants that, for practical purposes, are homozygous for all characters. Then he can continue reproducing them indefinitely with the assurance that the progeny will be like the parents. His basic procedure—though there are many necessary modifications and complications—is commonly the one given here.

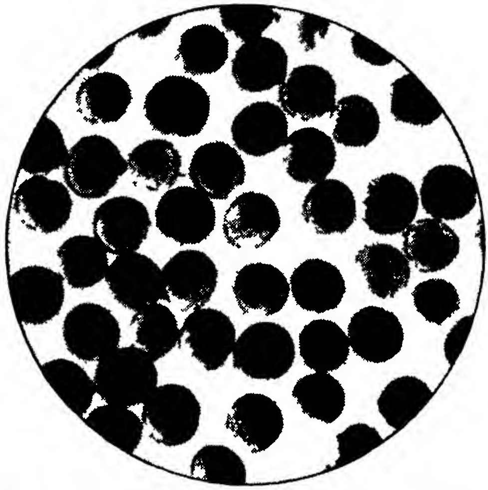

Figure 2.—An early effect of a gene on a characteristic is shown in these pollen grains from a sorghum plant heterozygous for the waxy gene. One-half of the pollen grains are waxy and stain red (light) with iodine, while the remainder are starchy and stain deep blue (dark). (Courtesy of Journal of Heredity.)

But what about the third type mentioned above— the plants with the tall–short combination in their cells? Here we have exactly the same combination we had in the F_1. In each cell of this type there is a chromosome containing the gene for tallness and one containing the gene for shortness. One-half of the reproductive cells, then, would get the gene for shortness and one-half the gene for tallness. Thus when the plants with the tall–short combination are inbred, they again segregate in the next generation into 1 tall–tall, 2 tall–short, 1 short–short. When an organism has two alternative genes for a certain character in its homologous chromosomes, it is said to be heterozygous for that character, as opposed to homozygous.

Effect of Dominance

So far, we have dealt only with what are called the genotypes of this tall–short combination in breeding. The segregation in the F_2 really took the form of 1 tall–tall, 2 tall–short, 1 short–short so far as the actual cells of the progeny were concerned. But it happens that with these particular characters of tallness and shortness there is a complication, namely, that tallness is a completely dominant characteristic and shortness a recessive. This means that when a cell contains the gene for tallness in one chromosome of a pair and the gene for shortness in the other, the tallness gene will dominate in the growth of the plant, and the shortness gene will, as it were, recede into the background.

We know that the cell actually contains both genes, but the plant does not show it so far as appearances go; it is a tall plant. In breeding terminology, its phenotype, which literally means its appearance type, is tall; its genotype, which literally means its breeding type, is tall-short. The genotype designates the actual genic constitution regardless of expression. The phenotype is the type that results from the interaction of the genes among themselves, as well as with the environment.

Thus in this case the phenotypic and genotypic ratios are not the same. All the plants with the tall–tall combination in their cells will of course be tall, but so will all the plants with the tall-short combination, because tallness is dominant. So far as the phenotype is concerned, then, the ratio becomes 3 tall plants: 1 short plant (the one with the short–short combination). This also is a simple phenotypic ratio, which is really only a modification of the genotypic 1:2:1 ratio and is produced whenever complete dominance is involved. Where there is no complete dominance, the segregation of the phenotype as well as of the genotype is 1:2:1. This occurs, for example, when the hybrid pink four o'clock, a flower, is selfed. The progeny segregates in the ratio of 1 red:2 pink:1 white.[6] Red in this case is partly dominant, but not enough to make plants with the red-white combination red in appearance. They are pink instead.

Another ratio that is a variation of the 1:2:1 was obtained by Cuènot, crossing yellow and black mice. The dominant gene, designated *Y*, produces yellow, and its allel, *y*, produces black.[7] Now it happens that when a cell received the homozygous combination *YY*, it could not live; that is, this gene was lethal for any cell that received it in both chromosomes of the pair. With only one *Y*, however, the cell could live. Thus in the segregation 1 *YY*:2 *Yy*:1 *yy*, the *YY* perished, leaving a ratio of 2:1. Since yellow (*Y*) was dominant, the phenotypic ratio was 2 yellow mice (*Yy*) to 1 black mouse (*yy*). There are many lethal genes in animals and plants that would give the same sort of results, but in most cases the lethals are recessives rather than dominants.

Such ratios are useful to the breeder in two ways. If he knows that a certain character is governed by a single pair of genes, he can tell what proportion of each type he will obtain in a large segregating progeny. When he does not know how many genes are involved in a certain character, he can find out, or obtain an estimate, at least, by figuring the ratio in the segregating progeny. If the character segregation is 1:2:1, he concludes he must be dealing with a single pair of genes and that complete dominance is not involved. If it is 3:1, he assumes it is a single pair of genes involving complete dominance. If it is 2:1, he knows it may be a single pair of genes, and that one of the alleles in the double condition is lethal.

[6] Knowledge of the 3:1 phenotypic segregation preceded that of the 1:2:1 as a phenotypic ratio. One of the first reports of the latter was made by Correns—German botanist and one of the rediscoverers of Mendel's original paper—working with the hybrid pink four o'clocks mentioned. There is no gene for pink, but the color is produced by the interaction of the whiteness and the redness genes in the same cell. The same result is obtained in the blue Andalusian fowl, which is produced by crossing a splashed white with a black. The segregation in the F_2 is 1 splashed white:2 blue:1 black. This ratio also occurs in commercial double carnations, produced by crossing the burster and the single varieties.

[7] The genetic formula is somewhat simplified. The designation is in accordance with the practice of designating a recessive gene by a lower-case letter and its dominant allel by the same letter capitalized.

Ratios With More Than One Pair of Genes

The situation becomes much more complicated when there are two pairs of genes and their alleles to be taken into account instead of one pair. Corn has been a favorite plant for studies of this kind. Figure 3 shows same heritable characters in corn.

Consider a pea plant with a pair of genes for tallness (*T*— dominant) and a pair of genes for red blossoms (*R*—dominant) crossed with a plant that has alleles (*t* and *r*) of these two genes and is dwarf (recessive) and white-flowered (recessive). The genotypic segregation, including all possible combinations of these two characteristics, would be like this:

Parents. Tall-tall red-red ×[8] dwarf-dwarf white-white The first parent indicated here would produce only gametes (germ cells) carrying genes for tall and red, while the second parent would produce only gametes carrying genes for dwarf and white. The progeny, F_1, of course, would carry both kinds of genes, that is, genotypically they would be tall-dwarf red-white; but in phenotypic appearance they would all be tall and red.

F_1: tall-dwarf red-white × tall-dwarf red-white. The gametes produced by each of the parents here would be of four kinds—tall-red, tall-white, dwarf-red, and

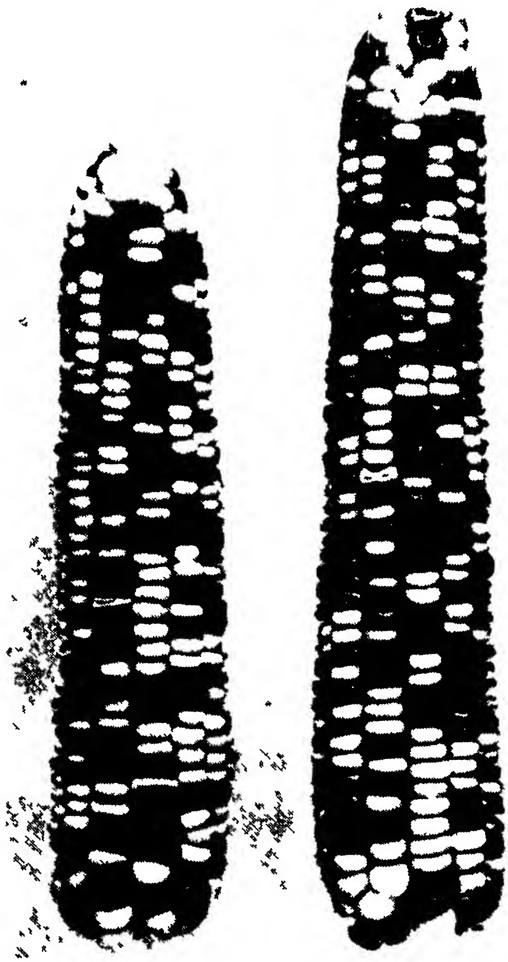

Figure 3.— Segregation for more than one character is shown on these ears of corn. It will be noted that there is not only a variation in color of the kernels but also a difference in the development of the kernels. Studies of heritable characters of this kind have enabled geneticists to increase their knowledge of heredity greatly beyond the fundamental laws formulated by Mendel. (Courtesy of Journal of Heredity.)

[8] The symbol × stands for "crossed with"

dwarf-white. These four kinds of gametes would unite by chance to give the various F_2 progeny. Possibly the best way to show the formation of these F_2 genotypes is by what is commonly known as the checkerboard square, presented below. The gametes produced by each parent are shown at the top and side of the checkerboard square. The genotype of each of the progeny formed by the union of all the different kinds of gametes is shown within the squares.

F_2.

Parent (gametes)

Parent (gametes)	*TR*	*Tr*	*tR*	*tr*
TR	*TTRR*	*TTRr*	*TtRR*	*TtRr*
Tr	*TTRr*	*TTrr*	*TtRr*	*Ttrr*
tR	*TtRR*	*TtRr*	*ttRR*	*ttRr*
tr	*TtRr*	*Ttrr*	*ttRr*	*ttrr*

Progeny (zygotes)

This F_2 checkerboard square adds up to the following genotypes: 1 tall-tall red-red: 2 tall-tall red-white: 2 tall-dwarf red-red: 4 tall-dwarf red-white: 1 tall-tall white-white: 2 tall-dwarf white-white: 1 dwarf-dwarf red-red: 2 dwarf-dwarf red-white 1 dwarf-dwarf white-white.

But tall is dominant to dwarf and red is dominant to white; that is, every plant with the tall-dwarf combination in its cells would be tall in appearance, and every plant with the red-white combination would have red flowers. Thus in the F_2, the segregation from the standpoint of phenotype or appearance would be

Tall red —9 (1 tall-tall red-red + 2 tall-tall red-white + 2 tall-dwarf red-red + 4 tall-dwarf red-white).
Tall white —3 (1 tall-tall white-white + 2 tall-dwarf white-white)
Dwarf red —3 (1 dwarf-dwarf red-red + 2 dwarf-dwarf red-white)
Dwarf white—1 (dwarf-dwarf white-white)

This 9:3:3:1 is the basic phenotypic ratio when two independently inherited dominant genes with their two recessive alleles are concerned.

Modifications of Basic Ratios

The basic ratios are modified in various ways. Interaction between the genes accounts for many of the modifications. It will be enough here to analyze five of the most common of these modifications through interaction.

(1) One dominant gene may have no visible effect unless a member of another pair is present. There is an example of this in corn, in which many color genes have been identified by R. A. Emerson and his associates at Cornell University. The dominant gene *R* governs red color, and its recessive allel *r* produces white. The dominant gene *Pr* produces purple, but only if *R* is present; otherwise it has no

effect. Suppose we have corn with the genes *r* and *Pr* (expressed as *r Pr*). This is white because, though it contains the gene for purple, *Pr*, it does not at the same time possess *R*. Let us cross this with a variety containing the genes *R pr*, which is red because it contains the *R* without the *Pr* that would modify it. Since the F_1 would have all the genes from both parents, its constitution would be *R r Pr pr*. It would be purple because it would have both *R* and *Pr*. The genotypes would work out in the 9:3:3:1 ratio already given—that is:

9 *R–Pr–*[9] (purple, because *R* and *Pr* are both present).
3 *R–prpr* (red, because *R* is present but not *Pr*).
3 *rrPr–* (white, because though *Pr* is present, it has no effect without *R*).
1 *rrprpr* (white—double recessive).

Thus the phenotypes add up to 9 purple: 3 red: 4 white, and we get 9:3:4 as the typical ratio for this kind of gene interaction.[10]

(2) Sometimes two dominants have a complementary effect on one another, but neither exerts any visible influence alone. Again we may turn to corn for an example. The dominant gene *C* and the dominant gene *R* produce colored (red or purple) kernels if they are both present, but neither has any effect alone. The recessive alleles, *c* and *r*, produce white. Suppose we have a variety with the composition *CCrr*, which is white because only one of the dominant genes is present, and another variety *ccRR*, white for the same reason. The F_1 contains the two dominants and the two recessives—*Cc Rr*—and is therefore colored. All the possible combinations would give us the following genotypes in the F_2:

9 *C–R–* (colored, because both dominants are present).
3 *C–rr* (white, because only one of the dominants is present).
3 *ccR–* (white, because only one of the dominants is present).
1 *ccrr* (white—double recessive).

Here the phenotypes add up to 9 colored: 7 white, and one concludes that 9:7 is the typical ratio for this kind of interaction.[11]

(3) Sometimes one dominant hides the effect of the other when both are present. In oats, the gene *G* produces a gray seed coat and the gene *B* a black seed coat, but the effect of *G* is always hidden if *B* is present. The gene *Y* produces a yellow seed coat, but only if neither *B* nor *G* is present. Suppose we cross a variety *BBGGYY* (black because *B* hides *G* and *Y*) with a variety *bbggYY* (yellow because *Y* is present but not *B* or *G*). The F_1 is *BbGgYY* and is therefore black. All possible combinations would give in the F_2:

9 *B–G–Y–* (black because *B* hides *G* and *Y*).
3 *B–ggY–* (black because *B* hides *Y*).
3 *bbG–Y–* (gray because *G* can show its effect without *B*).
1 *bbggY–* (yellow because *Y* is present without *B* or *G*).

This gives a phenotype ratio of 12 black, 3 gray, and 1 yellow—12:3:1 being the typical segregation for genes interacting in this way.

(4) Sometimes when there are two dominants, one acts as an inhibitor of the other. For example, in corn, *R* produces red kernels;

[9] The small dash (-) in the symbol stands for the presence of either the dominant or the recessive gene In this case, *R–* stands for *RR* or *Rr*, while *Pr–* stands for *Pr Pr* or *Pr pr*.

[10] In this particular example, there are really four other known genes present, A_1, A_2, *C*, and *i*. Together, these genes produce color when *R* is present, but they have no effect when *R* is not present. The real composition of the white parent, then, is $A_1A_1A_2A_2CCrrPrPrii$, of the red parent $A_1A_1A_2A_2CCRRprprii$, and of the purple F_1, $A_1A_1A_2A_2CCRRPrPrii$. Since A_1A_2Ci is the same in all three cases, it is omitted to make the analysis clearer.

[11] This example is also somewhat simplified in the genetic formula.

r white kernels; *I* prevents the action of *R*; *i* has no effect. Stated in another way, the recessive (*ii*) must be present to allow the gene *R* to be effective. Suppose a variety *rrii* (white, the double recessive) is crossed with *RRII* (also white because, though *R* is present, it is inhibited by *I*). The genotype of the F_1 is *RrIi* and is white. The F_2 segregates as:

9 *R–I–* (white because *I* inhibits *R*).
3 *R ii* (colored because *R* can act with *i*).
3 *rrI–* (white because *R* is not present and also because *I* is present).
1 *rrii* (white because R is not present).

The phenotypes here add up to 13 white: 3 colored.[12] This 13:3 phenotypic ratio is commonly called the inhibitor ratio, and the larger number always represents the gene that acts as the inhibitor.

(5) Finally, there may be two dominants, each having the same effect as the other, or as both of them together. In the common shepherds-purse, the seed capsule is triangular in shape if the dominant gene *C* or the dominant *D* is present—and also if both are present. If both the recessives of these genes, *c* and *d*, are homozygous, the seed capsule is top-shaped. Dr. Shull of Princeton crossed a variety *ccdd* (top-shaped) with a variety *CCDD* (triangle-shaped). From the triangular F_1 (*CcDd*) he obtained in the F_2:

9 *C D* (triangular both dominant genes present).
3 *C–dd* (triangular—one dominant gene present).
3 *ccD* (triangular—one dominant gene present).
1 *ccdd* (top-shaped—double recessive).

This adds up to 15 triangular: 1 top-shaped, giving a 15:1 ratio.

Other modifications of the ratio for two pairs of genes are: 9:6:1, 4:11:1, 1:11:4, 7:4:4:1, 1:7:4:4, 1:8:4:2:1.

When three genes with their alleles are involved instead of two, the ratios become still more complicated,[13] and they will not be illustrated in detail here. The basic phenotypic ratio in the case of three pairs of genes is 27:9:9:3:9:3:3:1. If the genes are considered as *ABC* and *abc*, this ratio is 27 *ABC*: 9 *ABc*: 9 *AbC*: 3 *Abc*: 9 *aBC*: 3 *aBc*: 3 *abC*: 1 *abc* Some variations in this basic ratio produced by the interaction of genes are 27:37, 27:9:28, and 63:1.

With more than three pairs of genes, the ratios become even more complicated, especially if there are complex interactions among the genes. It is evident that large numbers of progeny would be needed to furnish a population with proportionate representation of all classes. This need for large numbers of progeny is one of the difficulties in animal genetics, where there is reason to believe that many genes, interacting in a very complex way, are involved in what appears to be a simple characteristic such as high or low milk production.

Backcrossing and the Backcross Ratio

The backcross ratio is different from any of those previously explained. The backcrossing technique consists chiefly in crossing an F_1 or later progeny back to one of the original parents or to an individual recessive for whatever characteristic is under consideration.

[12] In this case also, the genes A_1A_2C are present in all the combinations, but they can be disregarded for the sake of simplifying the analysis

[13] It will be noted in the above examples that three pairs of genes are sometimes involved, or even more, but only two of them in both the dominant and recessive forms— that is, only two genes with their alleles.

The ratio is now being used to advantage by both the geneticist and the breeder. The genetic make-up of the sow shown in figure 4 is being tested by the backcross method. The geneticist uses it primarily to test for linkage, a phenomenon explained in the next few pages. The breeder uses it chiefly for two purposes—(1) to test whether a given character exists in a pure (homozygous) form or in a hybrid

Figure 4.—A backcross ratio obtained in a litter from a cross-bred Berkshire-Yorkshire sow by a Berkshire sire. The ratio is 7 white: 6 black with some white. Two of the latter type died. (Courtesy of Journal of Heredity.)

(heterozygous) form in one of the parents used in the backcross and (2) to transfer a valued characteristic such as disease resistance into an otherwise desirable variety that lacks it.

Suppose the breeder is dealing with a gene *B*, which produces black in Aberdeen Angus cattle and is dominant to its allel *b*, which produces red. He is not sure whether a given black animal is homozygous or heterozygous, since both *BB* and *Bb* produce exactly the same appearance. It is necessary for him to know, however, if he wants to go on breeding pure black animals, because if he picks two that are heterozygous the progeny will keep on segregating into blacks and reds. In order to test the composition of an animal by this method, he backcrosses it to a red individual, which, of course, has the double recessive, *bb*. In the following generations one of two things must happen. (1) All the progeny will be black, in which case he knows that the animal he was testing must have been homozygous, with the composition *BB;* for *BB* crossed with *bb* would give every offspring a *B* and a *b*, or *Bb*, which would make every animal black. (2) He might get an equal number of blacks and reds, in which case he knows that the uncertain animal must be heterozygous, or *Bb;* for *Bb* crossed with *bb* would give 1 *Bb:* 1 *Bb:* 1 *bb:* 1 *bb*, or 1 black: 1 red. In the first case, he can keep on using the animal he has chosen with the assurance that it will breed true. In the

second case he will have to discard the animal and its progeny if he wants a herd pure for black.

Backcrossing, especially with plants naturally selfed, is seldom resorted to for the purpose of determining whether they are homozygous for a given gene. A few progeny from selfed plants are all that are needed for this purpose, and, of course, in self-fertilized plants it is much simpler to self a plant, grow a few progeny, and note whether they segregate.

The 1 : 1 is a so-called backcross ratio, and it always appears when a recessive is crossed with a heterozygous individual. The backcross method therefore can be used to test the purity of any stock that exhibits a dominant character. Backcross ratios also have been worked out for two and three pairs of genes with their various interactions. For example, in the case of two genes, *A* and *B*, with their alleles, *a* and *b*, a heterozygous plant with the composition *AaBb* crossed with the pure recessive *aabb* would give 1 *Aa Bb:* 1 *Aa bb:* 1 *aa Bb:* 1 *aa bb.*

The second use of the backcross is to transfer a certain valued character to an otherwise desirable variety. Suppose the breeder has a plant, A, that has good commercial characteristics but is susceptible to a disease, such as bunt in wheat, and a plant, B, that is worthless commercially but has bunt resistance, a dominant characteristic. He crosses them, determines by suitable tests that the F_1 is resistant, inbreeds the F_1, and finds that the F_2 segregates into disease-resistant and disease-susceptible plants. He may backcross the F_1 to A, the double recessive for bunt resistance, and obtain the backcross ratio of 1 resistant to 1 susceptible. A second or third backcross may result in successfully retaining bunt resistance and at the same time getting all of the desirable characters of the susceptible parent, A. This backcross method is most successful when only one dominant factor is involved. When the resistant reaction is recessive, the backcross method of breeding is not so successful.

The important thing for the breeder to keep in mind here is that B contributes worthless commercial characteristics as well as the valuable one of disease resistance, and he must use skill in selecting the particular disease-resistant plants for backcrossing on A. They must have as many A qualities as possible, but, of course, lack susceptibility to disease. Too much emphasis cannot be placed on the importance of wise selection, especially in view of the fact that usually many genes are involved in even the simplest characters, rather than one dominant gene as in the above example.

LINKAGE AND CROSSING OVER

ALTHOUGH the discussion of ratios has dealt with genes, it should be kept in mind that the genes are located in chromosomes. Just what genes or chromosomes are, or by what means they exert their fateful control over the characteristics of organisms, remains an unsolved mystery of science. A chromosome may be thought of as merely an aggregation of genes that stick together, like a chain composed of a series of links, each somewhat different from the others; or as a spiral of protoplasm inclosed in a matrix and divided into sections, each section being a gene; or as a package containing

genes, like a druggist's vial containing pills. The point is that genes occur in groups; and since they do, all of the genes on one chromosome and the characters controlled by these genes tend to be inherited together in what is known as linked-inheritance or linkage.

This is quite different from the idea held by Mendel, the father of modern genetics. One of Mendel's laws was that all characteristics assort independently of each other in inheritance—the theory of independent assortment. As a matter of fact, apparently all the characteristics Mendel studied in peas were so located that they did assort independently. This was one of the most lucky of scientific accidents. If Mendel had happened to deal with linked characteristics or those involving the interaction of genes, the results might have been so complicated that he could not have worked out his clear-cut laws with the knowledge then available.

It was about 1905 when Bateson and Punnett in England discovered characteristics that did not assort independently but remained together in inheritance. As more evidence of this kind accumulated, various theories were proposed to account for it. The one finally accepted was that genes for certain characteristics tend to be linked together in what were called linkage groups. When Sutton in 1902 showed that chromosomes, the existence of which was known through microscopic studies of the cell, play the dynamic role in inheritance, it took only one more step to demonstrate that the genes in a linkage group are carried on a specific chromosome and the number of linkage groups and chromosomes is the same. Corn, for example, has 10 chromosomes and 10 linkage groups. However, it is not possible by looking at a chromosome to tell what genes it contains. The breeder must first discover by actual test what characteristics tend to be linked together in inheritance; then he assumes that the genes determining these characteristics are located in the same chromosome. In some cases, notably the pomace fly and the corn plant, it has been possible by such breeding tests to assign a large number of genes to definite chromosomes.

But the situation is not so simple as this account might indicate. A given gene does not always stay in the same chromosome. Kempton's article in the 1936 Yearbook described how a pair of homologus chromosomes become twisted together during the formation of reproductive cells, and how they may exchange equal portions during this process. This is called crossing over, and it is equivalent to saying that genes are exchanged between the two chromosomes. Thus the original linkage group is changed and a new combination within the linkage group is formed.

Suppose, to take an imaginary example, that on one chromosome there is a gene *A* determining resistance to a certain disease and not far from it a gene *B* determining broad leaves. In the corresponding places on the homologous chromosome of the pair, there is a gene *a* determining susceptibility to the disease and a gene *b* determining narrow leaves. When these chromosomes segregate in inheritance, every plant that is disease-resistant will have broad leaves and every one that is not resistant will have narrow leaves, since *AB* are located in one chromosome and *ab* in one chromosome. But suppose that in the reproductive cells of one plant, *A* and *a* are exchanged by crossing over. Now *Ab* will be in one chromosome and *aB* in the

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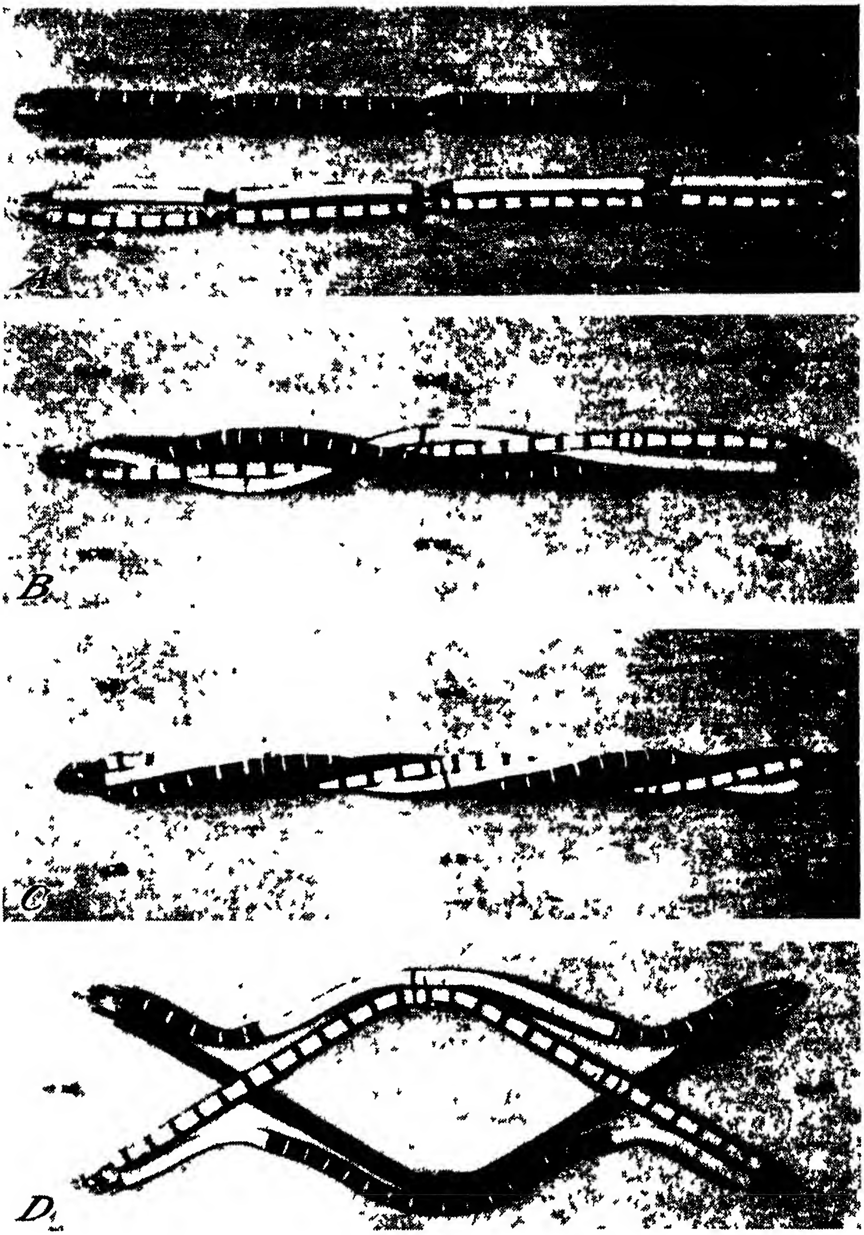

Figure 5.—Models of chromosomes (*A*) broken into "chromatids" (longitudinal sections), showing two ways (*B, C*) in which the sections might wrap around one another to produce the cross-overs shown in *D*. These chromosome models were prepared by H. B. Newcombe and G. B. Wilson, of the Department of Genetics, McGill University, Montreal, Canada. (Courtesy of Journal of Heredity.)

other, and there will be an opportunity to obtain new true-breeding strains as a result of these recombinations. Figure 5 illustrates two ways in which linkage groups are broken up by crossing-overs.

If the genes were very close together, the break would obviously have to occur within a very narrow range to bring about an exchange, and if they were next to each other it would have to occur exactly between them. In other words, the closer the genes are on a chromosome the less likelihood there is that a break will occur in the right place to make an exchange possible. Geneticists have taken advantage of this fact to locate the position of genes on chromosomes without actually seeing the genes. For example, if in a case of linkage 20 recombinations are obtained out of every 100 progeny, the two genes are said to be located about 20 units apart on the chromosome, for the number of new combinations that are obtained when linkage is involved depends upon the amount of crossing over, and this in turn depends on the distance of the genes apart. In this case the genes would be said to have 20 percent linkage, since the degree of linkage is designated by the amount of crossing over. Cross-overs are extremely frequent and they may make breeding operations either more difficult or easier, depending upon a breeder's desire for new combinations.

It is this physical fact that enables the geneticist to draw maps showing the locations of genes on chromosomes. First, by appropriate tests he determines that two genes, *A* and *B*, are located on the same chromosome. Then, by breeding many progeny, he determines the percentage of cases in which there is crossing over. By getting a whole series of percentages for other genes—*C*, *D*, *E*, *F*, *G*, *H*, etc.—in relation to both *A* or *B*, he can determine how close these are to the genes already located. Without ever seeing or identifying any of the genes, he can determine mathematically their relative position on the chromosome, and knowing the percentages of crossing over between them, he can make a genetic map of a chromosome showing the approximate locations of the genes. Other techniques are available for aiding in chromosome mapping.

Effect of Linkage on Segregation

The effect of linkage on segregation ratios may be illustrated with the fowl. Landauer and other investigators have demonstrated a linkage between the creeper characteristic, which causes a marked shortening of the long bones of the wings and legs (the fowl seems to creep), and single comb. Rose comb (*R*) is dominant, and single comb (*r*) is recessive. Creeper (*Cr*) is dominant, and normal or noncreeper (*cr*) is recessive. To show how this linkage affects ratios an example of an actual cross is given. One parent is normal and rose-combed (*cr cr RR*), the other is creeper and single-combed (*Cr cr rr*). The "creeper" parent is heterozygous for this condition because when homozygous it is lethal, the embryos dying at about the seventy-second hour of incubation. When these parents are crossed, one-half of the F_1 progeny have all four genes and are of the genotype $\frac{cr\ R}{Cr\ r}$[14]. They are creeper and rose-combed because of the effects of the two

[14] This form is used in linkage studies to designate which genes are linked. In this case *cr* and *R* are on one chromosome and *Cr* and *r* on its homologue.

dominants. Now the F_1's of this type are backcrossed on double recessives, that is, fowls with single comb and normal wings and legs, $\frac{cr\ r}{cr\ r}$. If the creeper and single-combed condition were assorted independently, we would get the normal backcross ratio—1 creeper rose comb: 1 creeper single comb: 1 normal rose comb: 1 normal single

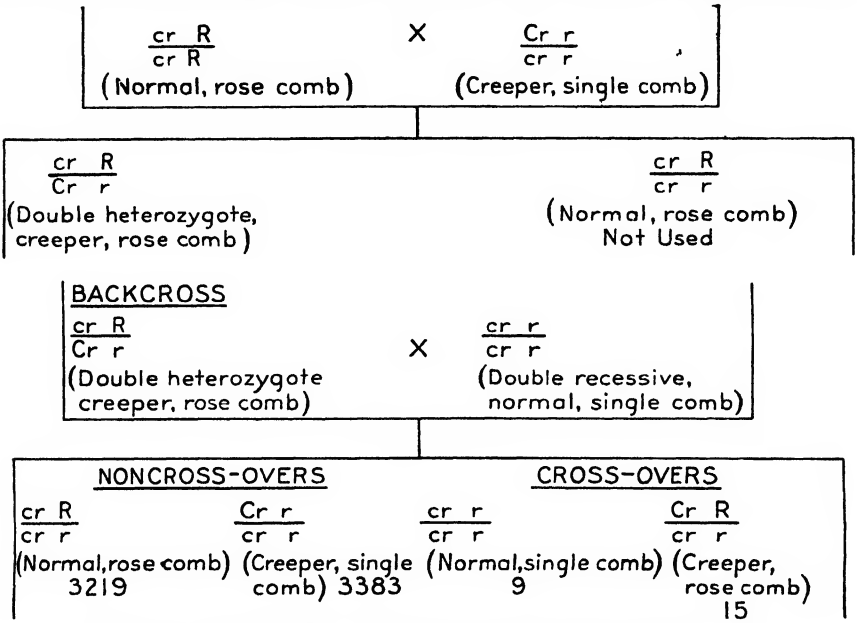

Figure 6.—Test for linkage between rose-comb and creeper genes.

comb. But this does not occur. Instead the following proportions, as shown by Landauer, are obtained—normal rose comb 3,219: creeper single comb 3,383: creeper rose comb 15: normal single comb 9. In other words, the normal rose comb and creeper single-comb birds (parental types) are enormously in excess of the number expected. The conclusion therefore is that the genes for normal wings and legs and rose comb are on the same chromosome, and those for the creeper condition and single comb are on its mate or homologue. When the chromosomes segregate, the original combination of genes stays together, and the few cases of the opposite combination are due to crossing over. Without crossing over there could not be a creeper bird with rose comb, or a normal one with single comb. Since 0.36 percent of the progeny were of these types, there must have been crossing over between the genes on the chromosome carrying the creeper rose comb characters and their alleles in 0.36 percent of the gametes produced by the parent heterozygous for both characteristics. This is referred to as 0.36 percent crossing over. The matings and segregations are shown in figure 6. The proportions were obtained by Landauer.[15]

[15] LANDAUER, W. STUDIES ON THE CREEPER FOWL. V. THE LINKAGE OF THE GENES FOR CREEPER AND SINGLE COMB. Jour. Genetics 26: [285]–290. 1932.

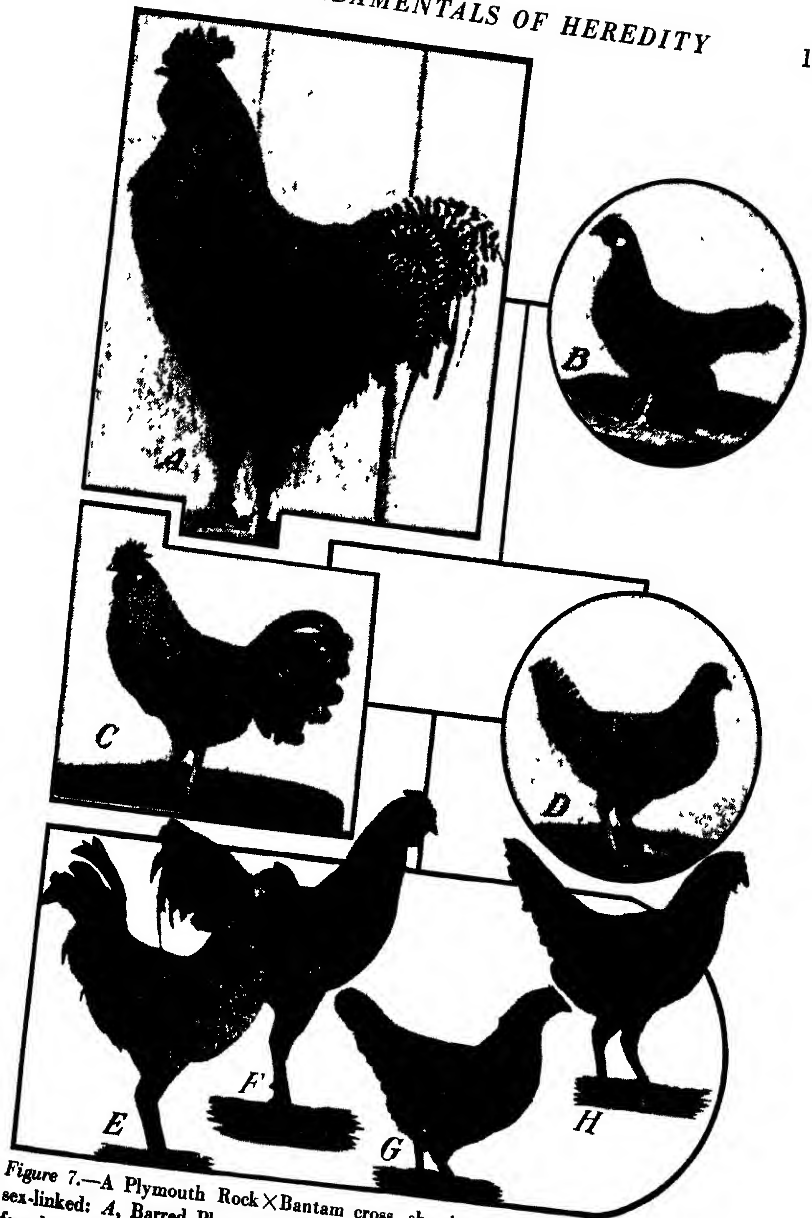

Figure 7.—A Plymouth Rock×Bantam cross, showing the barring gene, which is sex-linked: *A*, Barred Plymouth Rock male parent; *B*, Rose Comb Black Bantam female parent; *C*, *D*, first generation; *E*, *F*, *G*, *H*, second generation. Note that barring is dominant (no black birds in the first generation) and a 3:1 ratio is obtained in the second generation. There are, however, no black males in this generation.

Sex Linkage

A special case of linkage of particular importance is the linkage associated with sex. Maleness and femaleness may be considered to be characteristics just as truly as any others. If they were determined exactly like other characteristics, however, the world would be very different than it is. Suppose, to take a hypothetical case, that in animals there was a gene *M* for maleness and an allel *m* for femaleness. Whenever a male and a female—*MM* and *mm*—crossed, all the progeny would be *Mm*. If *M* were dominant, they would all be males, and no further reproduction would be possible. If neither gene were dominant, all the progeny would be male-female, that is, hermaphrodite. Neither of these conditions occurs; instead, in the population at large, males and females are born in approximately equal numbers. If sex is determined by a gene, then, it does not operate like other genes.

What actually does determine sex is another of the unsolved problems. It is known, however, that in many animals, sex is associated with a chromosome peculiarity. In the dog, the cat, the pig, the cow, the horse, and some other animals it is believed that the female has one more chromosome than the male. In these cases the male contains all the chromosomes contained in the body cell of the female, and in addition one so-called *X* chromosome—not a pair. The female, who has a pair of these *X* chromosomes, therefore always has one more chromosome than the male with *X*. In some species of *Drosophila*, each sex has a pair of sex chromosomes, but they are different in males and females. The odd chromosome found in the male is designated as *Y*, so that the female has the composition *XX* and the male the composition *XY*. In moths and birds, this situation is reversed; the male has a pair of sex chromosomes called *ZZ* and the female a single *Z* chromosome and a *W* chromosome. The effect of a typical sex-linked gene-barring is shown in figures 7 and 8.

If sex is determined by a gene (or even a number of genes in combination) on a sex chromosome, this arrangement would bring about a segregation that accords with the facts. Let us say the female is the one homozygous for sex, with the combination *XX*. The male is heterozygous, with the combination *XY*. When the chromosomes are reduced to form reproductive cells, every reproductive cell produced by the female has an *X* chromosome. Out of every two reproductive cells produced by the male, however, one has an *X* chromosome and one has a *Y*. When a female cell met an *X* male cell, the union would give the combination *XX*, which would become a female organism. The female cell that met a male *Y* would have the combination *XY*, which would become a male organism. In the *WZ* type of sex determination males are homozygous, *ZZ*, and females heterozygous, *WZ*. In both cases, males and females would be produced in approximately equal numbers in the population as a whole.

On the other hand, it is possible that sex is not determined by a gene or genes. One theory is that it is determined by a certain balance between all the chromosomes. There might well be a different

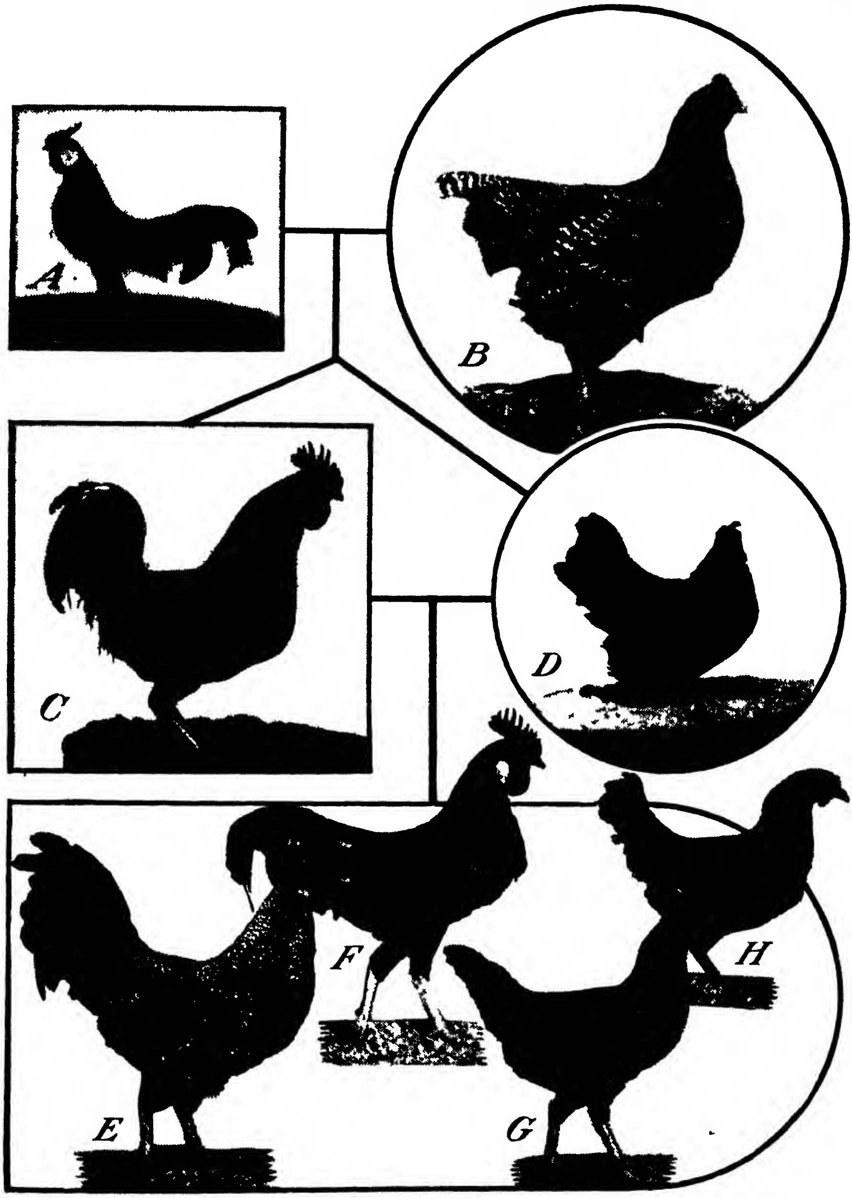

Figure 8.—The reciprocal of the cross shown in figure 7: *A*, Rose Comb Black Bantam male parent; *B*, Barred Plymouth Rock female parent; *C*, *D*, first generation; *E*, *F*, *G*, *H*. second generation. Note that in this cross the Black Bantam is a male and the Plymouth Rock a female. The color factors show typical sex-linked inheritance—also what is known as "criss-cross inheritance." The latter is common in cases of sex-linked inheritance. In this cross it is readily seen when the parental and first generation types are compared. The black color of the male parent is shown only in the female of the first generation and the barred characteristic of the parental female is shown only in the male. In the second generation there is an equal number of barred and black males and females, respectively.

balance between an organism with one *X* or one *Z* chromosome and an organism with two.

The sex chromosomes do more than determine sex (granted that they do that). They also carry genes determining other less unique characteristics such as barring, mentioned above. All the genes on a sex chromosome, naturally, are in a single linkage group, and they are associated with sex in inheritance. How does this work out?

As an example, we might take the type of color blindness in man that renders a person unable to distinguish between red and green. This is a sex-linked characteristic; it is recessive and its determining gene is located on the *X* chromosome. Now it has been shown that when an *X* chromosome from a female cell combines with a *Y* in the male cell, the result is a male organism, a son, On the other hand, when an *X* from a male cell combines with an *X* from a female, the result is a female, a daughter. This is another way of saying that a son can receive the *X* chromosome only from his mother. The father's *X* chromosome, on the other hand, can go only to the daughter. Thus if the father's *X* chromosome contains the gene for color blindness, it will go to his daughter but will be expressed only if both father and mother transmit color blindness, since the two recessives must come together. A son who is color blind could have inherited the trait only from his mother, from whom alone he receives the *X* chromosome.

A sex-linked characteristic, it should be noted, is quite different from a sex-limited characteristic. A sex-limited characteristic is one that can be expressed by one sex only; genes for it may be contained in the other sex, but there is something that inhibits its expression. Thus milk production may conceivably be inherited by both males and females, but its actual expression is limited to females. Horns in Rambouillet sheep are limited to males; presumably there is something in the glands of the females that inhibits the expression of horns, or perhaps something in the glands of the male that compels the expression.

MUTATION OF GENES AND CHROMOSOMES

OTHER phenomena in addition to linkage and crossing over affect the orderly transmission of a given set of genes to offspring. In a broad sense these phenomena may be classed as mutations. Gene mutations involve a change in one or more genes, and they are now understood to be caused in any one of a number of ways, as by heat reaching the cell at a certain stage of its development, or by radiations of certain wave lengths. In the latter case, it has been suggested that a gene may be altered by a direct hit from an electric particle. In any case, once a gene in a reproductive cell has mutated, it is thereafter inherited in the new form, unless there is another mutation, It is now commonly believed that many, perhaps most mutations, are harmful to the organism.

Polyploidy brings about similar results. This is an increase in the number of chromosomes in the cell, beyond the number that is normal for the particular organism. Polyploidy frequently occurs when organisms only distantly related are crossed. Presumably some or all of the chromosomes from the two parents are so unlike that they are

unable to join in pairs, with the result that the number cannot be reduced in the regular way when reproductive cells are formed. The unpaired chromosomes are then left over to increase the regular number in the reproductive cell. Sometimes there is only one extra chromosome, sometimes several, sometimes a whole extra set, or more than one extra set. The phenomenon is treated at greater length in Dr. Blakeslee's article, which appears in a separate of this Yearbook.

Naturally geneticists deal with other concepts besides Mendelian ratios, linkage, sex-linked factors, lethal factors, multiple allelomorphs, and other phenomena discussed in this article. They are paying considerable attention to such things as chromosomal aberrations, translocations, gene frequency, epistasis, and genetic tensions. As yet the real importance of some of these newer concepts is not known. Some may have a profound effect upon our knowledge of heredity, others may be of little importance or may prove to be another way of stating something that is already known.

The influence of environment on the expression of genes cannot be ignored. For instance, in the case of animals it is only under certain specific conditions of feeding, care, and management that genes for rapidity and economy of gain, or for high milk production, can be fully expressed. Taking production as an example, it is conceivable that one strain of dairy cattle might have genes that would enable it to produce at a high level on a diet that would reduce the production of another strain to a very low level. In other words, there is no universally optimum environment but an optimum for a specific gene or genes. Temperature and nutrition have been found to produce important effects even on such characters as coat color in rabbits and rats. In certain kinds of rabbits low temperatures cause new hair to come in black, whereas at higher temperatures the hair developing on the same parts of the body is white. Thus it is evident that the geneticist must consider the interaction of the genes with the environment in accurately describing their expression.

GENETIC ANALYSIS—PLANTS AND ANIMALS COMPARED

INTENSIVE study of one animal form, the small pomace fly of the genus *Drosophila*, principally by Thomas Hunt Morgan and his students, has contributed very largely to the understanding of the mechanism of heredity. Because of its short life span (it lives only 13 days on the average), its minute size, which permits hundreds of flies to be grown in small vials, its small number of chromosomes, and the presence in the species of a large number of different characters, it has proved to be remarkably good material for genetic study. But even with *Drosophila*, progress has been made at the cost of much painstaking labor, and probably over 25,000,000 flies have been raised and examined with meticulous care by students of this species.

With the laboratory rodents and the fowl progress has also been relatively rapid. The manner of inheritance of many traits, such as color and various defects of structure and function, has been clearly determined and it has been shown that the types of inheritance (independent, linked, and sex-linked) are the same for these forms as for *Drosophila* and many plants. And the masterful analysis by Wright

of the results of many years of inbreeding of guinea pigs by the Department of Agriculture has contributed much to what is known of the consequences of inbreeding, cross-breeding, and various other systems of mating, in both plants and animals.

With the larger animals progress has not been so great and the criticism is frequently made that genetics has contributed little of importance to animal breeding. Much of this criticism is unjustified. While the direct contribution to breeding practice has not yet been great, genetics has contributed in a large way to an understanding of the basic principles of breeding, and many concepts and superstitions, such as telegony (an alleged effect of a sire on later progeny of the same dam by another sire) and maternal impressions, have been discarded as a result. It is now possible more readily to eliminate undesirable hereditary traits from breeding stock. Application of this knowledge has been employed especially in the elimination of such abnormalities as lethal conditions, which have been found to be inherited to some extent in most classes of animals.

The way in which the breeder of dairy cattle, for example, is today shaping some of his breeding methods on the basis of genetic principles is greater than is ordinarily realized. Within a period of 10 years breed associations have adopted herd tests for the purpose of securing records on all animals in a herd instead of the best ones only—a recognition of the fallacy of selective testing. They are publishing daughter-dam records for sires in recognition of the need of determining the genetic make-up of outstanding sires. Great emphasis is being placed on the sire that has proved through the progeny test that he possesses a superior inheritance. Finally, many courses for the study of the principles of Mendelian inheritance as applied to dairy cattle are now held regularly.

In a negative way also genetics has contributed to practical breeding. A knowledge of Mendelian laws has brought an understanding of the consequences of the various systems of mating that have shown the limitations of selection and certain other breeding practices.

In plant production it is usually possible to obtain large numbers of progeny in a relatively short time and at little expense. The segregation by classes permits a determination of the ratios between them, and this makes it possible to formulate a hypothesis to explain the mode of inheritance and the genotype of the parents in a rather conclusive manner for most qualitative and some quantitative characteristics. By the application of the principles of Mendelism it has also been possible to work out the genetic basis for the more simply inherited unit characters in animals, explain the occurrence of unexpected progeny, and predict the frequency with which they may be expected in the future. With a background of such information the breeder can decide whether he wishes to continue to breed a dam that produces progeny meritorious in some such character as conformation even though a certain percentage of her progeny have a very undesirable characteristic and must be culled.

An understanding of the mechanism of sex determination was also largely dependent upon genetic discoveries. Cytologists had postulated the sex chromosomes as the basic sex-determining mechanism, but it remained for the discovery of sex-linked characters and the genetic

analysis of such characters to furnish final proof of the correctness of this hypothesis. In poultry a large number of sex-linked genes have been studied and the facts obtained from some of these studies have been put to practical use in certain crosses to determine the sex of chicks at the time of hatching. There is also some evidence that certain genes affecting such characters as maturity and rate of winter egg production are sex-linked, and, if these observations are substantiated, the information should eventually enable the poultryman to incorporate these genes more easily into his flock.

Aside from such rapid-breeding forms as *Drosophila*, Mendelian analysis with animals in the sense of locating individual genes or finding the number of genes that determine a given character will always be more difficult than with plants, and a complete analysis with the larger animals will probably never be made.

Why Progress in Animal Genetics Is Slow

There are numerous reasons why animal genetics has not made and cannot hope to make as rapid progress in working out a complete genetic analysis as has been possible with plants. Some of these reasons will be discussed below.

(1) The male and the female are different individuals. Thus self-fertilization, an important method used extensively in plant breeding, is not possible in the breeding of livestock. The progeny always has genes contributed by both parents, and since each parent has a different set of genes this greatly retards the rate of production of genetically pure forms. Progress in plant genetics has been aided by the ability to determine the genotype through the segregation of progeny produced by self-fertilization. The mating of brother and sister or of a parent to his or her offspring is an approach to the self-fertilization method used by the plant breeder, but the progeny test, as shown in figure 9, is being more and more widely used as a method of determining the genotype in animal breeding.

(2) The rate of maturity and breeding is relatively slow. In most plants with which genetic progress has been made, it is possible to obtain at least one generation a year. An animal— for example, a calf— must often be kept 2 years before it produces any progeny. In turn, the female progeny must be kept 2 years before it produces milk, in case this is the character to be measured. Another year is required to get the complete lactation. If the first calf happens to be a female, at least 5 years are required to get the first record of production on dam and daughter. Further records on other progeny will be needed to determine the genotype of the dam.

(3) The number of progeny of any pair of individuals is usually too small to be sure of the genotype of the parents. Earlier in this article, it was pointed out that the genotype of the individual is determined by the type of progeny it produces. Backcrossing to the homozygous recessive strain was found to be the easiest way to determine the genotype. Applying this to a dairy animal, let us assume that dominance is involved in inheritance of milk yield. If the animal in question were a cow and if a bull carrying the recessive factors were available, so many years would be required to get sufficient milk records on the female progeny of this cow in order to have data on which

sound conclusions might be based regarding the genotype of the dam that the procedure would be impracticable. Moreover, only half of the calves would be females, and not all of these would be raised so that milk records could be obtained for them.

A case of polled condition in cattle involving a single pair of genes will help to explain this, although it should be kept clearly in mind

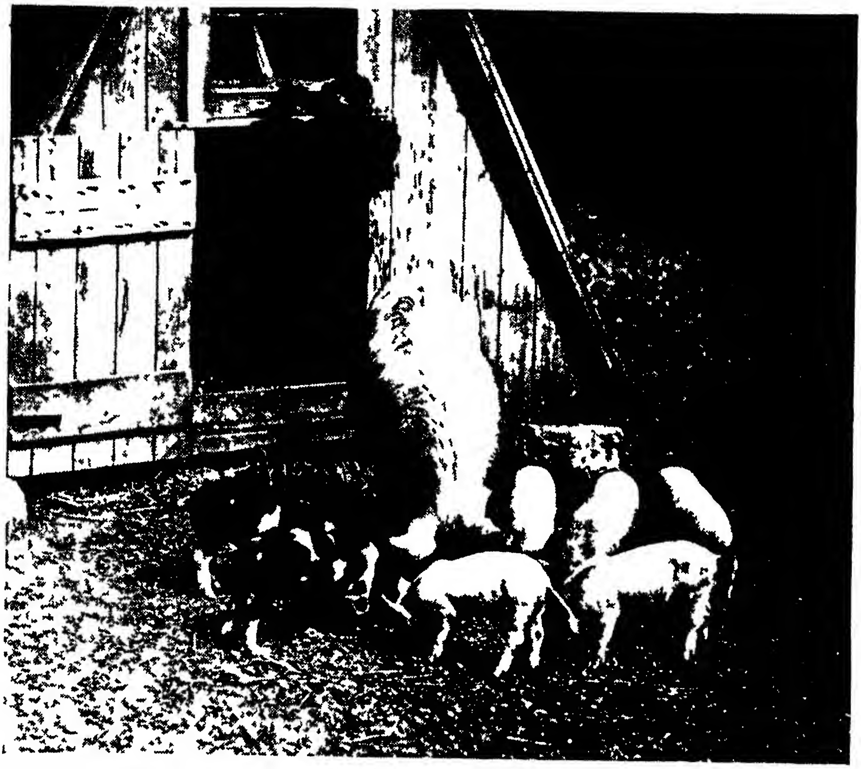

Figure 9.—Brother and sister matings are the closest approach that the livestock breeder can make to the self-fertilization method used by the plant breeder. Here is shown a cross-bred Berkshire-Yorkshire sow with pigs by a Yorkshire-Berkshire sire. The ratio is 7 white pigs: 2 black with some white. Both of the latter type died. (Courtesy of Journal of Heredity.)

that milk production is probably due to several pairs of genetic factors. In cattle the polled condition (*P*) is dominant and horns (*p*) recessive. Suppose a polled cow produces a polled heifer calf, but in later matings produces a horned bull calf (simple recessive). It is desired to know if the genotype of the polled heifer calf is *PP* or *Pp*. In the former case, the heifer might advantageously be kept for breeding purposes, but in the latter case, it might be undesirable to do this in view of the fact that she would transmit the gene for horns to one-half her progeny. Of course, she could be used for breeding purposes and produce no horned calves if mated to a *PP* sire even though the gene for horns would be transmitted to one-half her progeny.

After reaching sexual maturity, the polled heifer (*P*–) is mated to a horned bull (*pp*). If she carries horns, one-half of the calves should be horned. If all the calves are polled, it will be necessary to produce four to six calves to obtain a reasonable degree of assurance that the polled heifer does not carry the gene for horns. Here, it has taken several years to determine the genotype of the polled heifer for one pair of genes, which may be expressed in calves of either sex. Consider how much more complex the problem becomes when the characteristic concerned is due to the action of several pairs of genetic factors, expressed only by females and not by them until they have reached sexual maturity, as in the case of milk production or egg production. Further, a cow that has produced four to six calves will not be available very much longer for breeding purposes.

The case of horns involving the action of only one pair of genes is the simplest kind that will be encountered. Suppose we are concerned with the inheritance of characters behaving like comb type in fowls. Here, two pairs of genes are involved. The double recessive for both pairs of genes results in a single-combed bird. The dominant gene of one of the pairs produces pea comb and the dominant gene of the other, rose comb. When the dominant genes are present in both pairs, a walnut comb results. The ratios to be expected in cases where two pairs of factors are involved have been pointed out in the previous discussion. At least 16 individuals would be necessary to represent the segregating groups in the proportion in which they occur in the F_2 generation.

Warwick has suggested that inguinal hernia in swine is due to the operation of at least two pairs of recessive genes. This characteristic does not ordinarily appear in sows, although sows transmit the genes for it. To determine whether a sow transmits hernia, it would be desirable to mate her with a herniated boar (backcross) and ascertain if any of her male pigs were herniated. The ratios expected would depend somewhat on the genotype of the sow. If she did not transmit both recessive factors, none of the pigs would be herniated. Still we would not know whether she transmitted the recessive gene of one of the allelic pairs. If she were heterozygous for one pair of factors and homozygous recessive for the other pair—that is, with the constitution *Aa bb*—one-half of her male progeny from the herniated boar would have hernias. If she were heterozygous for both pairs of factors, with the constitution *Aa Bb*, one-fourth of the male progeny would be expected to have hernias. Modifying factors may still further complicate the situation. Therefore, it is usually considered advisable, instead of testing the individual concerned in a definitely planned experiment, to go ahead with the usual breeding operations, and if the parents produce herniated pigs, to assume that both parents transmit the undesirable characteristics, and discard them so as to eliminate the possibility that their progeny will carry an undesirable recessive to still more descendants.

The difference between high and low milk production certainly is due to the operation of several pairs of genetic factors. Estimates of different investigators have ranged from 3 to nearly 20 pairs of genes. This increases the number of animals necessary to give a complete segregating population beyond any possibility of a single pair of par-

ents producing sufficient progeny to determine the genotype accurately. With 10 pairs of genes, which has been suggested by Turner as the minimum number controlling milk production, 1,048,546 animals would be required to give a complete F_2 population and 1,024 progeny to give a complete backcross generation. Obviously, it is impossible to get enough progeny from matings between the same two individuals, yet genotypes of a pair cannot be ascertained otherwise. Moreover, to allow for chance variations, it is usually considered necessary to have at least three times as many individuals as are needed for the complete segregating population.

(4) Animal-breeding research is very costly. It is much more expensive to produce a single individual than would be required in the case of a single plant. Special care, feeding, management, and adequate space are required. The progeny of any single mating is small as contrasted with the large number of seeds produced by most plants. The cost of keeping the numbers of animals needed to work out a rather complex ratio involving several pairs of genetic factors is almost prohibitive.

(5) Many of the characteristics of economic importance do not readily group by classes. Color, horns, and many of the more obvious characteristics are inherited in a relatively simple manner, but the genetic basis for characteristics concerned with the production of milk, meat, eggs, wool, etc., is more complex. The genes determining milk-producing capacity may act in a cumulative manner, or dominance may govern their expression to a greater or lesser extent. It is probable that if several pairs of genes are involved, various kinds of gene interactions occur, which adds to the complexity of determining the mode of inheritance of such characters.

In cases where a large number of genes are operative in determining a quantitative characteristic such as yearly butterfat production, different genotypes may give rise to the same phenotype. For example, with genes *A*, *B*, and *C*, assuming that *A* was responsible for 150 pounds; *a*, 25 pounds; *B*, 75 pounds; *b*, 25 pounds; *C*, 100 pounds; and *c*, 25 pounds, one might have an individual producing 350 pounds of butterfat with the genotype *Aa bb Cc*, or *aa Bb CC*. Such conditions make the identification of the effect of the different genes very difficult, if not impossible. When a large population is needed in order to have representatives of the different types, the difficulties encountered in studying quantitative characters, which includes so many of those of economic importance, are apparent.

(6) Modifying factors, which play an important part in the inheritance of many characters, tend to spread the classes so that one grades into another. The mode of inheritance of these factors is similar to that of the other genes concerned, yet their presence may completely change the results obtained. For example, in some poultry there is an inhibiting gene preventing the appearance of any color. The presence of this gene results in the white of the White Leghorn. Yet the White Leghorn may carry many color genes, expression of which is inhibited until suitable crosses with other breeds permit their expression in the absence of the inhibitor. In quantitative characters, such genes may increase or reduce the expression of another gene, as in the case of the relative amounts of color and of white in spotted animals.

(7) Environmental effects may prevent the expression of certain genes. The characters of economic importance in livestock are influenced to a considerable extent by environment. For example, it is well known that a dairy cow may not produce up to her inherent capacity if she receives an insufficient food supply. To be sure, the plant is subject to environmental influences also, but ordinarily plants are placed under more adequate control, or at least the effect of environment can be evaluated more easily and at less expense. The identification of the role of the individual gene becomes practically impossible unless the environmental effects are known and kept constant.

Breeding Programs and the Future of Animal Genetics

Fortunately there is a brighter side to this picture. It is not necessary to know how many genes affect each character nor the effect of each individual gene entering into the final expression of a given quantitative character in order to make progress in animal breeding. Again we may use the inheritance of milk yield as an example. We now know that the cow that produces 350 pounds of butterfat cannot be depended on to transmit the inheritance for that level of production to all her offspring. But if a herd of such cows are mated to a certain sire and all or most of the daughters produce 400 to 450 pounds of butterfat under the same environmental conditions, then we know that the sire possesses a genotype for a higher level of production than did the dams to which he was mated. Furthermore, the continuous use of sires that have demonstrated through the progeny test that they possess a genotype for higher levels of production will result in concentrating the factors determining the higher levels of production in the germ plasm of the herd. (The genotype of the dam as well as that of the sire can be determined by the progeny test, but the time required is so much greater and the inheritance of the individual dam is transmitted to so few progeny that it is much more feasible to work through the sire.) Thus progress is made in animal breeding by working with the end result of numerous genes, even though the number of genes involved is not known, nor the part that an individual gene plays in bringing about the end result.

Research work is gradually bringing about a knowledge of the extent to which some of the more common environmental variations may influence the expression of a character. In dairy cattle, for instance, knowledge is being accumulated concerning the effect on production of a number of factors, including age; the use of box stalls as compared to stanchions; the number of milkings per day; different ratios of grain or the all-roughage ration. Such information helps in evaluating a sire when, as frequently happens, the dams and daughters did not make their records under entirely comparable conditions, since suitable corrections can be made. However, more knowledge is needed to solve many of the problems that confront such a system of breeding as that outlined above. For example, when a sire is mated to dams with a very high level of production and the daughters of that mating have a somewhat lower level of production than the dams, it is difficult to determine what the genotype of the sire is, unless he has also been mated to cows possessing a lower level of production to see whether

he raised it or not. Likewise, when a sire is mated to dams with a level of, say, 350 pounds of butterfat and his daughters prove to be considerably above that level, it is impossible to know whether he has a genotype that will enable him to improve the germ plasm of a herd of cows with an average level of, say, 600 pounds, perhaps made under different environmental conditions than the record of the first herd.

The so-called proved-sire system of breeding progresses most rapidly where (1) the sire is mated at an early age to a large group of females, so that there is a sufficient number of female progeny to make possible the evaluation of his genotype before he reaches too advanced an age; (2) there is no selection of the daughters and their dams on the basis of high records; (3) records are made under environmental conditions that are comparable for both daughters and dams; and (4) environmental conditions are sufficiently good to enable the animals to express levels of production approaching their inherent capacity.

The difficulties encountered with the breeding of larger animals as contrasted with the progress made with insects, plants, and laboratory animals lends support to the idea that it never will be practicable, or perhaps possible, to identify the action of each gene in animal breeding. Genetic principles may be worked out with laboratory animals or insects that may be kept at much less cost and will reproduce rapidly. In experiments with larger animals, the genes will not necessarily have to be identified, but evaluations may be made by methods analagous to those employed in proving dairy sires in order to determine transmitting ability. It makes little difference to the dairyman whether 350 pounds of butterfat is produced because the animal was of the genotype *Aa bb Cc*, *aa Bb CC*, or what not, except that crosses of strains of certain genotypes would be expected to produce animals superior to either parent. In practice, it probably would be more satisfactory to test the complementary action of the genes from different animals by trial crossing rather than to attempt to discover the specific genes carried by each animal and the part they play in determining and transmitting characteristics

The complementary action of unidentified genes has been successfully used with corn Strains have been inbred to insure that they were homozygous, and by trial and error it has been found that the progeny from certain crosses are superior to ordinary varieties. The practice of similar methods would appear to offer promise in animal breeding, though experimental evidence will be needed in order to determine whether the results would be superior to, or more reliable than, those obtained by the proved-sire system. Then too, when close inbreeding in animals results in a loss of efficiency in characteristics of economic value, as is often the case, the cost of maintaining these closely inbred strains for crossing will be much greater than is the case with inbred strains of corn. Not all inbred strains of corn respond with marked hybrid vigor when crossed, and many strains have to be crossed in order to find those that result in increased yields. If this same amount of work is necessary with livestock, the expense of this method of breeding appears quite formidable, particularly in the case of cattle and horses. With smaller animals, like swine, the limitation is somewhat reduced and in fact experimental work of this kind is rapidly getting under way.

With the larger animals it is apparent that breeding progress will come about largely through what might be called a mass determination of the genotype. By the application of the progeny test and the use of sires proved in that manner, it will probably be possible to produce strains of animals in the various species containing combinations of genes that will give better average production than any strains now in existence. This method, combined, perhaps, with some inbreeding to produce greater homozygosity of the desired characters, holds great promise for the improvement of all forms of livestock. Progress obviously will be slow, however, owing to the difficulties that have been enumerated.

That genetics has not contributed more to livestock-breeding practice is not surprising. As a science it is less than 40 years old, and many of the basic discoveries have been made in the last 20 years. But the principles underlying breed improvement have been determined, and progress in the future should be more rapid. While Mendelian analysis has taken first place in some forms of life, it is certain that with the larger animals such an analysis will remain secondary to the testing of various breeding systems with the aim of synthesizing better and better strains.

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VEGETATIVE REPRODUCTION

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ALL of the important fruit-crop plants in the United States, many of the ornamentals, a few crops like potatoes, and some of the nut and forest trees are multiplied or propagated for commercial production by vegetative means. This means that a new plant is developed from a vegetative portion of a mother plant, such as a cutting or bud, instead of from a seed, as is the case with most of the cereal, forage, and vegetable crops. This fact is extremely important from the standpoint of the principles and methods employed in the improvement of fruit crops by breeding.

As was explained in detail in the article on Heredity Under the Microscope, in the 1936 Yearbook, the seed in the ordinary plant develops from a single cell, the fertilized egg, which has received in the fertilizing process chromosomes from both the female or seed parent and the male or pollen parent. These chromosomes transmit the hereditary factors or genes from both parents, and the offspring that develops from this cell, therefore, inherits the characteristics of both. If the germ cells from the two parents carry genes that are alike for all characteristics, the plants that develop from the seeds will be very similar to these parents. On the other hand, if the parents transmit unlike genes for various characters, many of the offspring will vary widely from either parent because of the effects of dominance, recessiveness, or modifying factors.

In vegetative propagation the new plant also develops from a single original cell. Although the bud or other propagative tissue may consist of thousands of cells, at one stage of its development only a single cell was involved. This cell carries the same genes as the mother tissue from which it was developed, and the genetic characteristics of the new tissue correspond to those of the mother plant, except in the case of vegetative mutations, to be discussed later in this article. From the hereditary standpoint it may be said that the vegetative offspring of a plant is a part of that plant itself rather than a new individual.

The Winesap apple, for example, originated as a seedling about 200 years ago. The original tree has probably been dead for more than a century. Before that tree died, however, buds taken from it were grafted into other apple roots and these buds developed into new individual Winesap trees, the tops of which are genetically a continuation of the parent trees. Many generations of trees have been grown from this original Winesap, yet the characteristics of the Winesap

trees and fruits today are but little, if at all, changed from those of the original tree.

Varieties of European wine grapes exist today that are believed to have originated several hundred years ago. These grapes have come down to the present time practically unchanged in character because vegetative portions of the vines rather than the sexual portions or seeds have been used for propagating them. The Wilson strawberry, originated in 1852, is still grown to some extent in Oregon. It has been propagated by runner plants ever since its origin and after many vegetative generations is today apparently similar in all respects to the parent plant.

CELL DIVISION IN VEGETATIVE TISSUES

In many respects the division of a cell to form two daughter cells in vegetative tissue is quite similar to that described in the article on Heredity Under the Microscope for germ cells. Each vegetative cell consists of the cell wall, the cytoplasm, and a nucleus. The nucleus, while the cell is in the resting stage—that is, not in the act of dividing—contains numerous chromatin granules, just as the germ cells do. In the beginning stages of cell division these chromatin granules collect in threadlike bodies, which are the forerunners of the more definitely organized chromosomes. These threadlike bodies are usually more or less separate, though in some cases they appear to be arranged end to end. Later they break up into independent chromosomes.

At this stage one very important step occurs that does not occur in the same way in the germ cell. After the chromosomes are formed in the vegetative cell, each chromosome appears to split longitudinally into two parts, giving twice the original number. Each of these parts appears to function as an independent chromosome. After that, the process is like that in the germ cell. The two halves of each original chromosome migrate, one to each of two poles on opposite sides of the nucleus. These two groups of chromosomes, one at either pole, now reorganize as separate daughter nuclei, each similar to the original one. A cell wall is formed between the two daughter nuclei, and there are two complete cells instead of the original one. Each of these cells, however, has the same number of chromosomes as the original, whereas if they were germ cells they would have half the original number.

Apparently the genes, which are the carriers of hereditary factors in the chromosomes, are also divided in this process of longitudinal splitting of the chromosomes, and this gives each daughter cell exactly the same hereditary factors. If it were possible at this stage to isolate each daughter cell and develop from it a wholly new individual, the new individuals would be exactly alike genetically and both would be exact genetic replicas of the parent plant.

However, it is, of course, never possible to grow two plants and have them exactly alike even though they have exactly the same genetic make-up. The final size and shape of a plant depends upon two factors—its genetic make-up and its environment. It is never possible to have exactly the same environment for two individuals. Variations in nutrition, light exposure, moisture relations, or in other

factors in the environment will always make some difference in the ultimate development of individuals. Genetically, however, plants that develop from these vegetative daughter cells will have the same make-up that was contained in the parent cell from which they were derived.

But, even in the most nearly perfect mechanism there is always the possibility that it may not function exactly the same in every case. Thus in the division of thousands of cells there is the possibility that certain cells may not divide so as to give the daughter cells exactly the same genetic make-up. In the splitting of the chromosomes, for example, it might occasionally happen that certain genes would fail to split, in which case one daughter cell might have a certain gene while the companion daughter cell might lack it.

There is ample evidence in the horticultural field that abnormal cell division occasionally occurs in the vegetative development of the plant. When it does occur, if the cell concerned is one from which major portions of the plant develop, a so-called bud sport branch may arise, showing a different character, and this sport or mutant may be propagated by vegetative means. Thus, in an apple variety a gene for fruit color may be added to or taken from a chromosome in a dividing cell at the tip, giving rise to a "color sport branch."

In certain plants shoots arise, not from the continued division of a single cell at the tip, but rather from the divisions of many cells in a group. In such cases the mutant cell may affect only one portion of the new shoot. This may represent a sector running throughout the length of the shoot, in which case we have what is called a sectorial chimera or variation. Buds taken from that particular section will develop into plants showing the variation throughout.

Also, in certain plants mutations occur involving only the outer ring or rings of cells on the stem. These are termed periclinal chimeras. The thornless sports of blackberries are of this type. They reproduce true to the thornless type from propagations made from stem tissue as tip layers, since in this case the new bark develops as a continuation of the old, but not from root tissues, because in this case all the new tissues originate from deep-seated cells that carry genes for thorniness.

These mutations in the vegetative tissues may involve only one gene or they may involve several. Thus, not only color of fruit might be modified, but shape, texture, season of ripening, or chemical composition might be affected by such mutations. At rare intervals a doubling of some or all of the chromosomes may occur without nuclear division, followed by regular division thereafter. Such a mutation, which produces a permanent increase in the number of chromosomes in each cell, often results in marked variations in vigor, fruit size, quality, and other factors in the mutant tissue. The variations can be reproduced in practically identical form by vegetative propagation.

It is noteworthy, however, that in most plants these vegetative mutations occur very infrequently. Ten thousand buds taken from a grape variety may develop into as many individual vines with hardly an observable variation that can be attributed to a lack of perfectly regular genetic reproduction in the vegetative cells. The remarkable feature is not that occasional irregular cell divisions occur, but rather that the irregularities are so rare.

This fact is of tremendous importance from the standpoint of establishing fruit varieties. Once an individual plant is obtained, as a result either of hybridization or of selection, it is possible to reproduce that plant almost exactly by vegetative propagation. With seed-propagated plants, on the other hand, before a new variety can be established it is necessary not only to secure an individual plant that has the characteristics desired but to follow this with selfing or inbreeding until a group of plants is secured of proper genetic purity to come true in large proportion from seed. This long process of breeding to secure varieties that come true from seed is not necessary in the improvement of plants that are vegetatively propagated.

The fact that all fruit varieties are vegetatively propagated, however, is not an unmixed advantage to the breeder of fruit crops. The very fact that individuals can be reproduced by vegetative means has resulted in the selection of varieties without any regard to how nearly they reproduce true to type from seed. Furthermore, up to the present time much less study has been made of the hereditary make-up of our fruits as a group than of many of the seed-propagated crop plants. We can usually judge what characters will be transmitted in inheritance, in the case of seed-propagated varieties of sufficient purity, by the type of parent material. This is not always true of vegetatively propagated plants.

The Northern Spy apple, for example, in its vegetatively propagated form is large-fruited. Seed of this variety, however, produces mostly smaller apples. A particular variety of grape may be black, yet seed planted from this variety may produce white, red, or black grapes. The possibilities of our horticultural varieties as breeding stock can be determined only by trial. In actual experience it has sometimes been found that a variety having very valuable characteristics when vegetatively propagated does not tend to reproduce these characteristics in the seed offspring. On the other hand, certain rather mediocre varieties may prove superior as parents for the development of improved sorts by breeding methods.

Most of our tree fruits and some ornamentals are propagated by budding or grafting the desired variety on the roots of the same or closely related species. With our tree fruits, these roots are mainly developed from seedlings. With grapes and roses, the roots are also propagated vegetatively.

There is much need for investigations in the United States to determine the best rootstock to use with the various fruit and nut varieties. The use of the best rootstocks might greatly improve the vigor and longevity of orchards under certain conditions. For example, peach rootstocks resistant to nematodes in the South and in parts of California should result in longer lived and more vigorous trees. The development of grape rootstocks resistant to phylloxera has saved the vinifera grape industry of southern Europe and in parts of California. The development of apple stocks resistant to woolly aphis would be a great asset to apple growing in many parts of the world. The characters of the rootstock are second only to the characters of the variety in determining successful production of many of our fruit varieties.

DO VEGETATIVELY PROPAGATED VARIETIES "RUN OUT"?

Closely allied to this discussion of the relation of vegetative propagation to breeding is the question of whether or not such vegetatively propagated varieties last indefinitely. It was long held, even by horticultural authorities, that after a few generations of vegetative propagation, varieties gradually lose their superior characters, become less vigorous, and decrease in value until they are abandoned as commercial sorts. Andrew Knight, of England, probably the

Figure 1.—Potatoes in middle row were propagated from seed pieces infected with curly dwarf, one of the potato virus diseases. The rows on each side were propagated from healthy seed stock. Virus diseases transmitted by vegetative propagation undoubtedly account for the so-called "running out" of many varieties.

greatest horticultural authority at the beginning of the nineteenth century, believed that varieties "run out" under vegetative propagation. Potato growers strongly held to this view until recent years, because their varieties appeared to deteriorate rather rapidly. Until recently, most growers of vegetatively propagated plants believed that such propagation is a weakening process and that new varieties propagated from seed must be developed frequently if vigor, quality, and productiveness are to be maintained.

It is true that many vegetatively propagated varieties are popular for a plant generation or two and then pass out of the trade. However, there is no evidence that varieties have become progressively weaker owing to repeated vegetative multiplication. In some cases, varieties develop diseases that may be carried from the mother plant to the daughter through the bud, cutting, or runner plant. This is especially true of the virus group of diseases, and many varieties may have disappeared because of such transmitted infection. A number of virus diseases are known that affect potatoes (fig. 1), strawberries, raspberries, and other vegetatively propagated plants. An under-

standing of these diseases has come only in very recent years. Prior to a knowledge of these diseases it was natural that the grower would assume that the weakened or malformed plants, resulting from vegetative propagation from infected parent material, were "running out." By keeping the parent material for vegetative propagation free of disease, such deterioration can be prevented.

Other varieties are discarded because of changing preferences on the part of the consumer or because the plant may not be sufficiently

Figure 2.—Winesap apple trees still vigorous, productive, and producing good-quality fruit. The leading commercial apple variety of the United States, this variety has been propagated vegetatively since its origin almost 200 years ago.

hardy, vigorous, or disease-resistant to meet new demands. The Early Crawford peach is an excellent example of this. This variety, which originated about 100 years ago, is still identical with the original in all the characters that made it very popular 50 years ago. Today, however, it is little grown, despite its high quality. Other varieties have developed that are heavier yielders, that can be shipped and held on the market in better condition, and that are somewhat hardier.

The Esopus Spitzenburg apple is another example of a very high-quality dessert variety that is disappearing from American orchards because the tree is not hardy and is particularly susceptible to many diseases. Yet there is no reason to believe that this variety as propagated today is in any way inherently different from the parent tree of 150 years ago. It is still a vigorous tree and productive, if protected from low winter temperatures and diseases. In contrast, the most extensively grown apple in the United States today is the Winesap (fig. 2), which is believed to have originated at least 200 years ago.

Occasionally a variety may show a lack of stability under vegetative propagation, which leads to an abundance of vegetative mutations generally of one particular type. For example, in a number of strawberry varieties under vegetative propagation there has been a marked tendency to mutate to a yellow-foliage form (fig. 3). Such wholesale

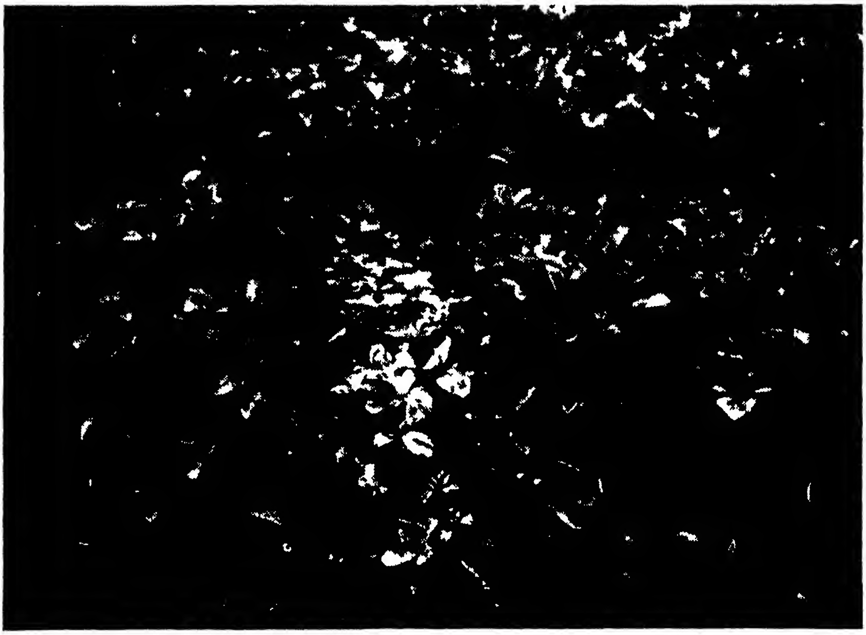


Figure 3.—The yellow-plant mutation (center) in the Blakemore strawberry. This mutation occurs very frequently in this variety and will result in the commercial deterioration of the variety unless propagating material is carefully selected to avoid it.

mutation has occurred in the Howard 17, or Premier, variety, and in recent years it has occurred in the Blakemore. Apparently some unstable gene occurs in the make-up of these varieties that develops a very high proportion of mutations. In certain strawberry varieties this has resulted in their passing out of commercial production.

The Washington Navel orange also appears to develop a rather large number of mutations under vegetative propagation. In most cases careful selection of the parent stock will permit the maintenance of such varieties. Perhaps this marked tendency to mutate, which occurs in a very few vegetatively propagated varieties, most nearly represents "running out" in the sense that the term has usually been employed. Even in this case, however, the selection of true-to-type parent material will usually maintain a variety indefinitely.

A CHRONOLOGY OF GENETICS

ROBERT COOK, Editor, Journal of Heredity

THE science of genetics as of 1937 has a long and rather involved history, which has not proved easy to treat as a chronology. Made up as it has been of a fusion of diverse specialties which have developed at different rates, a simple chronological listing of discoveries and developments necessarily gives a rather fragmentary picture of the unfolding of the modern science of heredity. Various plans were considered to avoid this difficulty, but the most satisfactory treatment seemed to be to combine everything in one simple chronology, which branches out into occasional summary paragraphs to suggest, without prohibitive chronological detail, the recent developments, and to buttress this with a graphic genetic family tree to give visually the relations of the various main components that have gone to make our modern genetic organism. The difficulties that have been encountered in determining many of the "first discoveries" noted in this chronology suggest that an exhaustive history of genetics will soon be necessary. Roberts and Zirkle have recently summarized the early publications on plant hybridization, but a connected story of the development of genetics as a whole remains to be written.

The compiler takes this opportunity to acknowledge invaluable help and suggestions from a group of about 35 geneticists who generously read and commented on a mimeographed first draft of this chronology. In the time allotted it would have been impossible without this freely given aid to have done nearly so complete a job as is here presented—which remains, it is regretfully realized, even with this help, only a very rough sketch. It was the wish of the editors to present in this Yearbook a bird's-eye view of genetic progress pointing out the important highlights but not in too much detail. Without overburdening this chronology with bibliographic references, and thereby reducing its readability to a minimum, and at the same time to make available authority for the dates given, a condensed list of references is included. A more detailed bibliography giving titles of articles cited and authors in full has been deposited in manuscript form in the United States Department of Agriculture library. Copies of this bibliography may be obtained from the library through the Biblioform Film Service. It is hoped that this will make all references reasonably easily available to all who are interested.

BEGINNINGS

FIRST hybrids were probably of species and varieties of cattle and dogs, by Neolithic people, possibly as much as 10,000 to 25,000 years ago.

Several varieties of dogs and of cattle and sheep are depicted on Egyptian and Babylonian monuments of 5,000 years ago. The bisexual nature of the date palm was also recognized by the early Babylonians and Assyrians 5,000 years ago. Mules are mentioned in Homer (B. C. 800) and in Herodotus (fifth century B. C.). The writings of Aristotle and other ancients abound in a wealth of observations, many of them confirmed by modern experiments. Unfortunately they also contain much very fanciful material—descriptions of astonishing and highly improbable hybrids between a great variety of animals. This very likely meant no more than that monstrosities were ascribed to hybridization, as the ancients generally looked upon the process of hybridization with abhorrence. Even angels and demons were reported on excellent authority to have produced hybrid progeny whose astonishing characteristics were limited only by the imagination of the narrator. Theories of heredity were not lacking, but facts that might verify these purely speculative fabrications were held in small esteem. Vergil tells us that the chosen seed, improved through years and labor, was seen to run back, unless man selected by hand the largest and fullest ears (Georgics I: 197). Columella and Varro also affirm the need for selection of cereal varieties. Theophrastus and Pliny discussed sex in plants but reported no experiments.

Allusions to the tendency of "like to beget like" are not hard to find in ancient literature. The Middle Ages enthusiastically added much to the fables but nothing to the factual background of the ancients. In spite of the lack of theoretical background, animal breeding, based on traditional methods ("like begets like" and various approximations to the progeny test), excellently exemplified in the New Testament aphorism "by their fruits ye shall know them", (Matthew 7: 20) made very considerable progress.

That primitive men have been not only persistent plant breeders but fairly successful ones is evidenced by the remarkable progress made in plant breeding in many parts of the world. The ancient Chinese are credited with breeding superior varieties of rice and hybrid flowers. Russian workers have recently published most interesting accounts of the wheat breeding on the southern slopes of the Caucasus Mountains. We have only to consider Indian corn, and the remarkable varieties produced by the American Indians, to realize the fact that man has been breeding plants from very early times.

The records left by the Babylonians and Egyptians leave no doubt that at least 5,000 years ago distinct breeds of domesticated animals were recognized. Certain of the types depicted on those ancient monuments bear a remarkable resemblance to modern breeds. Excellent types of beef cattle and of merinolike sheep are to be seen in some of these ancient relics, which mark the beginnings of recorded history. Jacob's famous agreement with Laban regarding "goats that were ringstraked and spotted" (Genesis 30: 35) has often been cited as evidence of an early belief in maternal impressions. But we read in the next verse that Jacob relied on "three days' journey" between Laban's solid-colored "cattle" and his own spotted flocks, and when it is explicitly stated that the rams used were spotted, it is clear that this ancient Hebrew herdsman did not depend entirely

on magic to produce results in animal breeding. Early Hindu writers also discussed these matters at length.

While the philosophers and scholars of the Middle Ages were piling one improbability on another, at least two great modern breeds were being formed—the Arab horse and the merino sheep. The desert horse had very remote beginnings, and it had reached or maintained such a state of excellence by the Middle Ages that it contributed greatly to the development of the horse of today. The English Thoroughbred breed traces to two Arab horses and a Barb imported into England about the time of Charles II. From very remote beginnings the Spanish merino had reached a perfection that gave Spain virtually a monopoly of the fine wool weaving industry by the fifteenth century. This monopoly was maintained by a strict embargo. Through royal courtesy the ban was lifted in 1765 to permit the export of merinos into Saxony. Within a few years merinos were exported from Spain to several other countries. In 1786 the famous merino herd at Rambouillet, France, was established. Maintained continuously since that time with only one importation of outside blood, this herd has formed the basis for the modern Rambouillet breed, which today is spread over all the world and is raised in greater numbers than any other type of sheep.

One other "root" of modern genetics also had a very early beginning. Mathematics was a subject intensively studied in Babylon, Egypt, and Greece. Some branches of the science of numbers were highly developed among the ancients, although algebra, so essential in modern genetic experiments, was not well developed until after the Crusades. This early science of numbers formed the groundwork for the later development of statistics, probability, and correlation, all necessary tools of modern genetics.

BACKGROUND

By the beginning of the seventeenth century a new spirit of scientific skepticism had begun to be manifest. The reaction of common sense against the cumulative absurdities of centuries of uncontrolled verbalism was reflected in the first stirrings of an age of scientific experiment. Nehemiah Grew in 1676 suggested the nature of ovules and pollen. A growing interest in biology culminated in the publication in 1694 of Camerarius' (Germany) famous 50-page letter on the sex of plants (De Sexu Plantarum Epistola), which put on record convincing evidence that plants are sexual organisms. This was followed early in the eighteenth century by the production of the first artificial plant hybrid by Thomas Fairchild (in England a short time before 1717). The practical implication of these discoveries is reflected in the founding in 1727 of the seed-breeding establishment today world-famous as Vilmorin-Andrieux et Cie. (One of the early great successes of the Vilmorins was the development of the sugar beet during the Napoleonic era.) In the next 50 years there was a veritable wave of hybridizing. Crosses between more than a dozen different plant genera were made by several investigators and reported with varying degrees of accuracy. This period culminated in the publication of J. G. Koelreuter's work (Germany, 1761–66), reporting the results of 136 experiments in artificial hybridization. This

mass of evidence definitely established plant hybridization as a scientific pursuit.

At the same time independent progress was being made in fields that after 1900 were to have a profound influence on genetics. M. Malphigi (Italy) was laying the groundwork for descriptive embryology (1650–70). A. von Leeuwenhock (Holland) was discovering the tiny world of the miscroscope, and with his pupil, Johan Ham (Holland), in 1677, was the first to see mammalian germ cells (spermatozoa). In 1780 L. Spallanzani (Italy) attempted to demonstrate by artificial insemination in dogs the essential part played by the male in fertilization.[1] The modern science of statistics had its beginnings at about the same time, in a treatise published in 1761 by a Prussian divine, J. P. Süssmilch, who undertook by appeal to vital statistics to prove the glory of God. The leisurely progress of scientific thought is suggested by the award to Linneaus (Sweden) in 1760 of a prize for an essay on sex in plants—nearly a century after Camerarius had rather conclusively laid the groundwork of this subject. Linnaeus' publication of Species Plantarum in 1753, which attempted to classify plants according to their assumed relationships, marks an important step in the development of evolution theory. In 1760 Robert Bakewell (England) took over the management of the Dishley Estate, where for 35 years he proved to his own satisfaction that inbreeding is not necessarily injurious and that it is the quickest way to fix type. His experiments laid the groundwork for the development of many of the modern breeds of livestock. In 1793 C. K. Sprengel (Prussia) observed the cross-pollination of plants by insects.

In the matter of human heredity some knowledge had also been accumulating. From the earliest times resemblance in relatives had been noted. The inheritance of such definite anatomical peculiarities as the "Hapsburg jaw" had frequently been recognized. Man has never been well adapted for laboratory study, and little exact progress was made. A notable exception has to do with sex-linked inheritance. The peculiar inheritance of color-blindness was reported to the Royal Society as long ago as 1779 by a British divine, Michael Lort. Forty years later C. T. Nasse (Germany) formulated a law of sex-linked inheritance based on hemophilia, a disease of unusual interest because of its occurence in the royal families of Europe.

By 1760 the stage was set for a century of biological progress that culminated in 1859 with the publication of Darwin's Origin of Species.

GENETICS IS BORN, 1760–1900

1760–1830—Foundation of important livestock breeds through inbreeding and selection practiced by English breeders—Bakewell, Bates, the Collings, and others.

1809—Publication of J. B. P. de Lamarck's Philosophie Zoologique (France) represented the first attempt to produce a comprehensive theory of evolution. Erasmus Darwin (England), G. L. L. de Buffon (France), and W. von Goethe (the German poet whose Metamorphosis of Plants, 1790, is a notable milestone in biological thinking) had dealt with various phases of the problem of organic development of individuals, species, and genera. Lamarck attempted to weld these observations and speculations into a coherent theory of evolution, an important step in biological progress.

[1] His "proof" that the fluid and not the spermatozoa was the fertilizing agent was unfortunately wrong. Not until 1824 did Prevost and Dumas correct this mistake.

1812—(1) Karl Friedrich Gauss (Germany), Theoria combinationis observationum erroribus minimis obnoxia (theory of least squares—basic in the statistical evaluation of data).

(2) Pierre Simon Laplace (France), Theorie analytiques des probabilités. Beginning of "the law of error concept."

1820—(1) Gauss, evolution of the probable error—for a century the almost universally used test of the significance of experimental data.

(2) C. F. Nasse (Germany), Nasse's law of male sex-linked inheritance, based on study of hemophilia.

1822—John Goss (England) reports but does not interpret dominance and recessiveness, and segregation in pea hybrids.

1823—Thomas Andrew Knight (England), Knight-Darwin law of cross-breeding (value of crossing to produce better plants). Dominance, recessiveness, and segregation observed in peas without mathematical relationships.

1826—A. Sageret (France) classifies contrasting characters in the parents of a cross in pairs, using muskmelons and cantaloups, cites unit characters in human eye color, and uses the term "dominant."

1835—(1) Division of cells described by H. von Mohl (Germany).

(2) Publication of K. F. von Gaertner's Memoir (Germany) reporting 25 years of hybridization experiments dealing with 107 species of plants; noted distinction between the uniformity of first hybrid generation and the diversity of later generations, and reported hybrid vigor.

1838–39—Cell theory, M. J. Schleiden and T. Schwann (Germany). First generalized statement of the theory that all organisms are made up of cells—one of the great generalizations of experimental biology.

1840—Word "protoplasm" coined by J. E. Purkinje (Bohemia), though used in a slightly different sense from that of today. A. Payen (France) and F. Cohn (Germany) suggested the essential similarity of protoplasm as the physical basis of all life (1846–50).

1841—R. A. von Kolliker (Switzerland) proves that spermatozoa arise from parent body and are not parasites as was previously believed.

1840–50—Louis de Vilmorin (France) develops the progeny test ("genealogical selection") in wheat, oat, and sugar-beet breeding.

1843—John Le Couteur (island of Jersey) publishes a summary of his work on wheat breeding. "This summary has been the basis and origin of variety testing" (De Vries). The same methods were independently developed somewhat earlier by Patrick Sheriff (Scotland), who produced many outstanding varieties.

1846—(1) A. Quetelet (Belgium), Lettres . . . sur la Theorie des Probabilités. Described biological phenomena in quantitative terms.

(2)Von Mohl recognizes nature and importance of protoplasm in its present sense.

1848—W. Hofmeister (Germany) figures the chromosomes as unstained bodies, but without appreciating their significance.

1849—(1) Sir Richard Owen (England) enunciates principle of the continuity of the germ plasm. This idea was developed by Virchow, Weismann, and others, and culminated in the modern gene theory.

(2) Union of sperm cell and egg cell (fertilization) first seen in seaweed (*Fucus*) by G. Thuret (France). A year later he showed that the egg would not develop without fertilization.

1858—R. Virchow (Germany) enunciates the principle: Omnis cellula e cellula (every cell from a cell), finally disposing of the theory of spontaneous generation—a basic biological generalization which completed the cell theory, establishing the continuity of all life from remote beginnings.

1859—Publication of Charles Darwin's Origin of Species (England). This contains extensive discussions of hybrids, but its contribution to genetics was mostly indirect. It marks a turning point in scientific thought and dates the beginning of the modern experimental approach to biological problems.

1861–62—M. J. S. Schultze (Germany) and H. A. de Bary (Germany) establish the essential unity of protoplasm in all living cells.

1863—D. A. Godron and C. V. Naudin (France) independently report experiments in plant hybridization. Naudin confirmed Sageret's work, in general discussed work of the early hybridizers, and reported dominance and segregation in *Datura* (jimsonweed) hybrids. He did not deal with single characters and reported no statistical observations on the second generation. His theoretical explanation of his facts was a forerunner of Mendel's ideas, but inferred rather than deduced.

1865—F. Schweigger-Seidel and A. von la Valette St. George (Germany) independently prove that a spermatozoon is a single cell and contains nucleus and cytoplasm.

It is impossible to tell how much of this earlier work was known to Gregor Mendel. Very likely most of it was. The work of Godron and Naudin was jointly awarded a prize by the French Academy of Sciences, so that it must have been fairly well known in scientific circles. Mendel had access to a rather extensive library, which included all of Darwin's works, and many other books on plant hybridization, etc. He was in contact with such eminent biologists as Nägeli, so that there is an excellent possibility that he had the benefit of this earlier work. But be that as it may:

1866—(1) Gregor Mendel (Austria) publishes in the Proceedings of the Brünn Natural History Society (Verhandlungen der Natur Forschenden Verein in Brunn) his investigations concerning plant hybrids, Versuche über Pflanzen-Hybriden, one of the oustandingly lucid and detailed expositions of a fundamental discovery. For 34 years Mendel's papers lay forgotten.
(2) E. Haeckel (Germany) predicts that the cell nucleus will play a star role in heredity.

1867—(1) Vilmorin tests immediate effect of pollen.
(2) H. S. Bidwell (United States) reports controlled pollination in maize.

1868—Darwin's pangen hypothesis—gemmules (hypothetical particles that float in the blood stream) are given off by cells and held to modify germ cells.

1873-4—L. Auerbach (Germany) begins experimental study of cell mechanics (fertilization).

1875—(1) E. Strasburger (Germany) describes the chromosomes.
(2) Oscar Hertwig (Germany) proves that fertilization consists of union of two parental nuclei contained in the sperm and ovum. This demonstration that sexual reproduction is a process contributed to essentially equally by the two sexes marked an important advance. It disposed of speculation regarding the role of the two sexes in inheritance, and it showed that genetics is basically a problem of cell physiology.

1878-81—W. J. Beal (United States) determines increased yields of corn hybrids between varieties and suggests their use in corn production.

1879-82—W. Flemming (Germany) describes the longitudinal splitting of the chromosomes.

1881—W. O. Focke (Germany) coins the term "xenia" to denote immediate effect of pollen on the endosperm in the maize seed.

1883—(1) P. J. van Beneden (Belgium) begins study of early history of animal egg. Reports reduction of the chromosome number in the egg cells to half that in body cells and holds that chromosomes have a genetic continuity throughout the life cycle—basically important concepts in genetic theory.
(2) E. L. Sturtevant (United States) observes without interpreting first linkage of genes now known as tunicate and sugary (*TuSu*) in maize.

1884—K. W. von Nägeli (Switzerland), ideoplasm concept—control of heredity seen as due to "ids", which were conceived to be solid particles. Nägeli's book was important as a precursor of Weismann's The Germ Plasm.

1884-5—(1) Identification of the cell nucleus as the basis of inheritance "made independently and almost simultaneously by Hertwig, Strasburger, Kölliker, and A. Weismann" (Germany).
(2) Halves of split chromosomes shown going to opposite poles by Flemming and others.

1885—C. Rabl (Austria) announces the individuality of the chromosomes.

1886—(1) Francis Galton (England) devises the correlation table—a most useful tool in applying statistical methods to many biological problems.

(2) Hugo de Vries (Holland) discovers aberrant evening primrose plants at Hilversum, Holland. Experiments with these extending over 15 years formed the basis for his mutation theory of evolution.

1885–87—Weismann publishes a theory of chromosome behavior during cell division and fertilization which explains earlier observations of Van Beneden, Strasburger, etc., and predicts that two kinds of cell division will be discovered—mitosis (already known) and reduction, in which the chromosome number will be reduced to half by an orderly separation of paternal and maternal chromosomes.

1887—W. Roux (Germany) suggests that the longitudinal splitting of the chromosomes when dividing means that many different qualities are arranged single file in the chromosome, and that these are all contributed by this method of division to each daughter cell.

1887-88—Th. Boveri (Germany) verifies Weismann's prediction of the reduction of the chromosomes by observing the phenomenon in *Ascaris*.

1888—Chromosomes named by W. Waldeyer (Germany).

1889—(1) De Vries revises the "pangen" theory of determiners floating in the blood stream, and denies any transfer of gemmules (determiners) from body cells to gametes.

(2) Francis Galton (England) publishes Natural Inheritance, which formulates his law of ancestral inheritance—a statistical statement of the relative influence of parents, grandparents, etc , in determining characteristics in offspring.

1890—(1) Law of numerical equality of paternal and maternal chromosomes at fertilization in animals and plants (Boveri, Germany; L. Guignard, France).

(2) Babcock test for butterfat percentages (United States). Beginnings of dairy-cattle selection for butterfat production on scientific basis.

1891—(1) Willett M. Hays (United States) develops the centgener progeny test, thereby recognizing that the test of the genetic quality of an individual can be adequately evaluated only by a study of its progeny. At about the same time the New York (Cornell) Agricultural Experiment Station develops rod-row method of small grain testing.

(2) W. A. Kellerman and W. T. Swingle (United States) make first count on a segregating ear of maize.

1892—With publication of Das Keimplasma (The Germ Plasm) Weismann enunciates the then very radical principle of noninheritance of acquired characters, and expands Nägeli's idioplasm theory to bring cell theory and "genetic theory" into organic relationship. Basing his theory on Van Beneden's observations. Weismann explains the reduction division as a method of exactly distributing the chromosome material.

1894—(1) W. Bateson (England) emphasizes the importance of the study of "discontinuous variation" (an approach toward the idea of Mendelian units) in solving the problem of heredity.

(2) Karl Pearson (England) publishes first of Contributions to the Mathematical Theory of Evolution, developing methods of dealing statistically with skew frequency curves.

(3) A. Millardet (France) notes "false hybrids" entirely resembling pollen parent (patrogenesis).

1897—(1) G. Udny Yule (England), publications On the Theory of Correlation.

(2) First egg-laying contests (England).

1898—(1) Pearson develops Galton's Law of Ancestral Heredity and also introduces the standard deviation, an improved method of determining the significance of deviations of observed data from theoretical perfection.

(2) S. G. Navashin (Russia) discovers double fertilization in higher plants.

(3) W. J. Spillman (United States) notes segregation in wheat, which he reported in 1901 in an independent statement of Mendelian principles.

(4) G. M. Gowell (United States) installs 52 trap nests and initiates scientific breeding for egg production.

(5) Flemming counts human chromosomes, finding 24 in corneal (eye) tissue. (Later work with improved technique shows 24 pairs.)

1899—(1) L. Cuénot (France) working with animals, and Strasburger (Germany, working with plants, advance theory that sex is controlled within the germ cell, not by environment.

(2) De Vries and C. F. J. E. Correns (Germany) publish almost simultaneously an explanation of xenia in corn as due to double fertilization

(3) First International Conference of Hybridization (the later conferences in this series were called Congresses of Genetics) held in London

EARLY DAYS OF GENETICS

THE TURN of the century was an epochal year in the experimenta study of heredity. The almost simultaneous rediscovery of Mendel'. paper independently by three investigators (who had, when they reac' Mendel's paper, experimental material of their own to verify hi: conclusions), was a striking symptom of an even wider trend. Batesor had for years been attacking the problem of discontinuous variation and Haldane says that had not Mendel's paper been discovered, Bateson would undoubtedly have been buried in Westminster Abbey as the discoverer of atomic heredity. Spillman's wheat work in the United States had reached a point where he appears to have been just on the brink of making the same illuminating generalization. Other workers also were hot on the trail of the gene, and the time was ripe for a veritable explosion of genetic progress. Within 3 years of the triple De Vries-Correns-Von Tschermak announcements, abundant verification of Mendel's work had been made by many workers, and the universality of the Mendelian principles had been demonstrated in plants, animals, and man. The fecund pomace fly, *Drosophila*, was about to enter his milk-bottle kingdom and populate acres of banana-agar nutrient medium with an ever-growing progeny of mutant forms. Into the hands of the research investigator had been given the key to unlock that perennial mystery of the ages, heredity

1900—Rediscovery and verification of Mendel's principles independently b De Vries (Holland), Correns (Germany), and E. von Tschermak (Austria) marking the beginning of modern genetics.

1901—(1) H. Henking (Germany), F. C. Paulmier (United States), and other report an "accessory chromosome" in spermatozoa (later identified with se determination), based on work begun in 1891.

(2) Bateson publishes a translation of Mendel's paper.

1902—(1) Terms allelomorph, homozygote, heterozygote, F_1, F_2, coined by Bateson. In their report to the evolution committee, Bateson and Saunders list 26 instances of allelomorphism which had been "actually provedt to exist, or may be inferred from the published record." This included cases in peas, wheat, maize, *Datura*, *Oenothera*, snapdragon, mouse, fowl, catle. The Mendelian nature of polydactylism (an extra finger) in man was suggested.

(2) De Vries—The Mutation Theory of Evolution, based on studies of evening primrose.

(3) T. H. Montgomery (United States) announces the pairing of homologous maternal and paternal chromosomes during synapsis (joining and separation prior to formation of germ cells with reduced chromosome number).

(4) E. C. McClung (United States) relates an accessory chromosome found in some insects to sex determination—first attempt to connect a specific character with a particular chromosome. The concept of specific sex chromosomes, which have a major influence in determining sex, has been verified, with modifications, in a range of organisms extending from the pomace fly to man.

(5) Cuénot first demonstrates Mendelism in animals (normal and albino mice).

1902—(6) Bateson defends Mendelism against attacks of W. F. R. Weldon and Karl Pearson (England). This heated clash regarding the utility of experimental versus statistical approaches to biological problems continued intermittently until 1904. Publication of first number of Biometrika, the leading journal dealing with the statistical aspects of genetics.

1902–3—W. W. Sutton (United States) shows that body chromosomes are individually recognizable and points out the mutual interrelations between cytological observations and Mendelian phenomena, closing the gap between cytology and genetics.

1903—(1) Pure-line concept (variations in the progeny of a single plant of a self-fertilized species are not due to inheritance) first put forward by W. L. Johannsen (Denmark). Phenotype and genotype defined. Modern concept of "selection" born.

(2) R. H. Biffen (England) reports that resistance to stripe rust of wheat is governed by a single Mendelian recessive factor.

(3) Bateson (walnut, rose, and single comb in fowl) and Cuénot (albino and pigmented mice) note interaction of nonallelomorphic factors (later called epistacy).

1904—(1) C. B. Davenport (United States) confirms Mendelian inheritance of polydactylism in man.

(2) American Breeders Association founded under Secretary of Agriculture James Wilson, with Willett M. Hays as secretary.

(3) Thomas Hunt Morgan becomes professor of zoology at Columbia University. This represents the beginning of the former "Columbia group" of genetic research workers, which included many of the names outstanding in genetics today. Other centers also had their origin about this time, at Harvard University, the University of Chicago, the University of Indiana, and Leland Stanford University.

(4) Station for Experimental Evolution established by the Carnegie Institution of Washington.

(5) A. F. Blakeslee (United States) reports isolation of sex-different strains of molds. First called "plus" and "minus", these were later called "male" and "female" though no morphological differences could be found between them.

1905—(1) G. H. Shull and E. M. East (United States) begin independent experiments on inbreeding in maize that opens up a field of the utmost theoretical and practical importance.

(2) N. M. Stevens and E. B. Wilson (United States) confirm McClung's sex-determination theory.

(3) "Coupling" (linkage) in sweet pea analyzed by Bateson, E. R. Saunders, and R. C. Punnett (England). Bateson and Punnett explain the walnut comb in the fowl as being due to two dominant factors, one of which alone produces pea combs, and the other, rose combs—the double recessive being single combs. This first report of interaction of Mendelian factors marked a very important advance.

(4) O. F. Cook and W. T. Swingle (United States) publish diagram and propose names for the sexual cycle (sporophyte-gametophyte) in plants.

1906—(1) Term "genetics" coined by Bateson.

(2) C. W. Woodworth and W. E. Castle (United States) "discover" *Drosophila*. "More has been learned concerning heredity from this one species since 1910 than had been learned from all sources before that time." It produces 25 generations a year and has but 4 pairs of chromosomes, so that it is ideally suited to make linkage studies. The modern gene theory is based largely on studies of *Drosophila*.

(3) Possible relation between linkage and the chromosomes pointed out by R. H. Lock (England).

(4) George Rommel begins U. S. Department of Agriculture inbreeding experiments with guinea pigs, which have been continued ever since.

1907—(1) Correns advances theory of two kinds of male gametes (male-determining and female-determining).

(2) J. B. Norton (United States) publishes rod-row system of breeding, first put into general use by him in 1902.

(3) Strasburger uses terms haploid and diploid for reduced and double number of chromosomes.

1907—(4) A. M. Lutz (United States) shows that the gigas mutation of the evening-primrose has double number of chromosomes of *Oenothera lamarckiana* Ser.

The discovery of a tetraploid in the evening-primrose opened up the subject of variation of chromosome number in general, and of polyploidy in particular. This discovery that organisms might vary in their chromosome constitution by an entire set of chromosomes has today developed a very extensive branch of cyto-genetics. Discoveries of polyploid series in wheat, the roses, the *Daturas* and *Solanums*, and elsewhere have marked a distinct advance in our understanding of the development of species. The artificial production of polyploids by heat treatment and by other means has been a more recent development of great promise. Even greater in its possibilities may be the production of generic polyploids (amphidiploids) having one or more complete chromosome complements from each parent species. These forms are generally self-fertile but are usually sterile with the parent species or genera.

(5) Bateson coins terms "epistatic" and "hypostatic" to describe interrelations of non-allelomorphic genes.

1908—(1) Cuénot discovers that the yellow gene (*Y*) in mice is lethal, suggesting that it kills the embryo early in development when inherited from both parents.

(2) Zeitschrift fur induktive Abstammungs-und Vererbungslehre (Journal for Inductive Descendence and Inheritance Theory) founded.

(3) Delaware Agricultural Experiment Station begins inbreeding experiments with swine.

Many practical breeders before this time had used intensive inbreeding in their operations, but the degree of inbreeding actually practiced is very hard to determine. Several instances are on record of herds being maintained for a number of generations without the introduction of new blood. N. H. Gentry's work with Berkshire swine in Missouri was a notably successful example of the use of inbreeding in breed improvement. The Delaware experiment represents the first attempt to attack this problem in a scientific manner with farm animals. All of the swine inbreeding experiments (and they are practically the only experiments in the intense inbreeding of livestock, by brother×sister matings, that have been undertaken, though considerably more has been done with poultry) have been only partially successful from a practical standpoint. The hoped-for production of highly inbred lines of swine that could be crossed to utilize to the full the principle of hybrid vigor in the first generation has failed to materialize because of the practical difficulties encountered in maintaining the inbred lines. Theoretically there appears to be no reason why robust inbred lines cannot be produced as has been done with rats and guinea pigs. Among the outstanding later experiments are those at the University of California, the Oklahoma Agricultural Experiment Station, Iowa State College (poultry), the Minnesota Agricultural Experiment Station, and the United States Department of Agriculture.

Many less direct attempts to produce highly inbred herds of livestock have been started and are continuing. Notable among these is the United States Department of Agriculture's development in dairy-cattle breeding, which has continued since 1912. The intention is to produce dairy sires pure or homozygous for high production by

line breeding as intense as possible to the foundation sire of the herd. While many practical breeders have used this method with livestock for short periods, this continuing project, with accurate records for many generations, is unique.

(4) H. Nilsson-Ehle (Sweden) explains that inheritance of color of seed in wheat is largely due to three Mendelian factors—multiple factors and blending inheritance begin to be added to Mendelian concepts. This principle was confirmed a year later by East in corn.

1909—(1) Crossing-over hypothesis (exchange of segments in paired chromosomes) advanced by F. A. Janssens (Belgium).

(2) R. A. Emerson (United States) reports multiple allelomorphs (more than one alternative factor) in beans and maize.

(3) Sir Francis Galton's bequest to found the Galton Laboratory at the University of London establishes the first laboratory devoted to the study of human heredity.

(4) Shull suggests use of first-generation hybrids between inbred lines as a basis of practical corn breeding.

1910—(1) L. Epstein and R. Ottenberg (United States) point out that human blood groups (discovered by K. Landsteiner, Austria, in 1900 and classified by Jansky, Germany, in 1907) follow Mendelian principles in inheritance.

(2) Morgan proposes explanation of sex-linked inheritance; publishes first gene mutation in *Drosophila* (white eye).

(3) Announcement of the gene theory by Morgan, which includes the principle of linkage of genes resident on the same chromosome. This brilliant hypothesis has been upheld in a multitude of experiments. Beginning of chromosome maps compiled by linkage and cross-over data.

(4) A. B. Bruce, and F. W. Keeble, and C. Pellew (England) suggest that hybrid vigor is due to dominant favorable growth factors.

(5) A. Lang (Switzerland) suggests multiple factor hypothesis to account for size differences in rabbits.

(6) H. Winkler (Germany) publishes method of producing *Solanum* chimaeras artificially. The explanation of these chimaeras as layers (periclinal) and sectors (sectorial) of cells from stock and cion was furnished by Erwin Baur (Germany) 1914.

1911—(1) Journal of Genetics (England) established

(2) Raymond Pearl (United States) publishes the first of his studies of egg production in the fowl.

(3) G. N. Collins and J. H. Kempton (United States) report first linkage in maize.

(4) Baur publishes the first edition of his Introduction to the Experimental Study of Heredity, Einfuhrung in die experimentelle Vererbungslehre.

(5) Richard Goldschmidt (Germany) publishes the first edition of his Einfuhrung in die Vererbungswissenschaft (Introduction to the Science of Heredity), which summarizes his theory of sex determination as a matter of rate of developmental expression of sex-determining genes—demonstrated by the production of intersexual forms in hybrids of the gypsy moth.

(6) W. E. Castle and J. C. Philips (United States), ovary transplantation experiment in the guinea pig, showing nonmodification of genetic characters through change in embryo environment.

(7) Cuénot, explanation of multiple allelomorphism in mice.

1912—(1) R. R. Gates (England) identifies *Oenothera semi-gigas* Vries as a triploid—the first to be recognized (triploids have three sets of chromosomes).

(2) H. S. Jennings (United States) shows that with self-fertilization the percentage of heterozygosis is halved in each successive generation.

This principle was elaborated by H. D. Fish (United States 1914) and Pearl 1913–17, and expanded by Jennings in 1917. In 1923 Sewell Wright (United States) published a general inbreeding coefficient applicable to irregular systems of mating. Since that time the evolutionary implications of Mendelian heredity have been developed by Wright, R. A. Fisher, J. B. S. Haldane, and others.

1913—(1) C. B. Bridges (United States) reports nondisjunction of sex chromosomes (both sex chromosomes going to one gamete and none to the other). Important confirmation of chromosome theory.

(2) Nils Hansson (Sweden) publishes first formula for a sire index, an improvement in the progeny test for characters not expressed by the sire.

More recently the sire-index idea has been elaborated by a number of suggested modifications of Hansson's original idea. All of these are based on the concept that the sire's transmitting ability for a character he does not himself show (such as milk or egg production) can be measured by comparing the production of his daughters with that of their dams. This concept is one of the bases of the "proved-sire movement" started in 1918 by the United States Department of Agriculture, which attempts to discover and to utilize to the maximum the sires that transmit desirable qualities to the greatest degree.

1915—Morgan, A. H. Sturtevant, Bridges, and H. J. Muller (United States) publish The Mechanism of Mendelian Heredity—an epoch-making book.

1916—(1) Castle confirms Lang's multiple-factor hypothesis of blending inheritance in rabbits.

(2) Winkler produces polyploid forms from the callus tissue of decapitated grafts

This method of doubling, tripling, and quadrupling the chromosome number has been rather widely used in experimental procedures by other workers. By applying it to haploid tomatoes, E. W. Lindstrom (United States, 1927) was able to obtain a pure line by doubling of identical chromosome complements—a procedure of considerable value in genetics and plant breeding.

(3) Castle and Wright discover first linkage in a mammal (rat).

(4) Pearl demonstrates effectiveness of pedigree selection contrasted with mass selection in the fowl.

(5) Shull suggests the word "heterosis" to designate the vigor of first-generation hybrids.

1917—(1) O. Winge (Denmark) elaborates theory of polyploid origin of new species by multiplication of a basic chromosome complex.

(2) Emerson finds variegated pericarp in maize due to an unstable gene.

(3) The Connecticut Agricultural Experiment Station produces the first commercial "crossed corn."

Following the early experiments of Beal, and the inbreeding experiments of Shull and East, inbreeding experiments with maize enjoyed a considerable vogue. It was found that where some of these uniform but usually rather unpromising inbred lines were crossed, an extremely vigorous and uniform first-generation hybrid was produced, which exceeded the yields of commercial varieties by 30 percent or even more. The production of this crossed corn seed on a commercial basis was first attempted at the Connecticut Station. Unfortunately the lack of vigor and the small quantities of seed produced by the inbred strains made seed production difficult and expensive. To obviate this difficulty the system of "double-crossed corn" (suggested by D. F. Jones in 1919, first commercial production attempted in 1921 by George S. Carter, Clinton, Conn.) was perfected, whereby four inbred lines were used. These lines (designated A, B, C, D) are crossed in pairs (A×B and C×D), and the resulting two extremely vigorous hybrids are crossed to produce the commercial seed. These varieties have great vigor and uniformity, and production of seed in commercial quantities is entirely feasible. Many workers have con-

tributed notably to this development, among them D. F. Jones, H. A. Wallace, F. D. Richey, and M. T. Jenkins, and many others in the United States Department of Agriculture and in the Corn Belt experiment stations.

The concepts developed by inbreeding have been applied in other ways, such as that of shifting a single desirable character from one variety to another by crossing and then by repeatedly back-crossing, to the other parental variety with the majority of desirable characteristics, those segregates that have the one desired character. H. V. Harlan and M. L. Martini (United States) first used this technique in barley in 1922, and it has been applied with equal success by several other workers.

(4) W. B. Kirkham, H. L. Ibsen, and E. Steigleder (United States) prove the lethal action of the yellow gene in the mouse by embryological studies.

The attempt to trace the beginnings of gene effects in the earliest possible stages of development (and to follow through to maturity the developmental history of a gene) has grown into a new and promising but often very difficult branch of genetic research—the "genetics and development" studies. The problem has also been approached by experiments in the transplantation of tissues and organs, by hormone injections, and by studies of the gene chemistry involved in color development of hair, etc. The field is just beginning to be explored.

(5) J. Jeswiet (Netherlands) working in Java proves that the Kassoer sugarcane (used in breeding mosaic-resistant P. O. J. hybrid sugarcane) is a second-generation hybrid of true sugarcane with a wild grass, *Saccharum spontaneum* L., that contains little or no sugar. This initiated large-scale sugarcane breeding in many countries, with wild relatives used to secure disease resistance. Later researches showed that the vigorous, disease-resistant, high-yielding sugarcane hybrids all showed a much higher chromosome count than true sugarcane (polyploidy).

1918—H. D. King (United States) reports results of inbreeding rats for 25 consecutive generations, showing that close inbreeding is not necessarily deleterious, and that fertility and vigor can be maintained in some lines.

1919—Morgan and others publish The Physical Basis of Heredity, setting forth in detail the gene theory, and summarizing *Drosophila* genetics.

RECENT DEVELOPMENTS

Even from the safe vantage of a third of a century it is not easy to evaluate the developments that followed the rediscovery of Mendel's work. As we advance nearer to the present our task becomes more difficult, for discoveries that now seem not especially revolutionary may, in the light of later work, be as epochal as Mendel's pioneer contribution. The time is too short to place a final value on many advances, and progress is being made on too many fronts to attempt to cover adequately the multitudinous work in genetics and related sciences. Some recent developments that may have been overlooked may be much more important 20 years hence than they seem today. Thus the compiler is sure only that in this most hazardous part of his journey he is treading on very dangerous ground indeed.

It was planned in compiling this chronology to avoid mention of any names in this final part, simply citing significant developments and trends, letting the perspective of the years determine more fairly

those who have made fundamental contributions to genetic progress. In practice this has proved difficult, because some names are so closely linked to certain discoveries that anonymity seems unfair. Thus radiation genetics and salivary-gland chromosomes immediately bring to mind the names of the pioneers whose work has very recently led the way to new bonanzas of genetic facts. Certain developments have been so interesting and significant that to stop the chronology 10 or 15 years ago purely through the promptings of the instinct of self-preservation would destroy much of its interest and value. The following compromise, which attempts to maintain perspective at very short range, is put forth with many misgivings and with a painful realization of the hazards involved. In the short summary paragraphs frequently interspersed with names and dates, an attempt has been made to suggest the extent and significance of some of the important developments.

1920—(1) Tobacco variety "made to order" by genetic methods (East and Jones in the United States).

(2) H. D. Goodale's (United States) studies of effects of selection on egg production.

(3) E. B. Babcock (United States) begins *Crepis* investigations, which are adding much to our knowledge of chromosome evolution within a genus.

(4) G. Tackholm (Sweden), monograph on polyploid series in *Rosa*, suggesting how a genus may have evolved through changes in chromosome number.

1921—(1) Triploid discovered in *Drosophila* by Bridges.

(2) Morgan estimates that the gene has a diameter between 20 and 70 microns.

Since Morgan first attempted to estimate the size of the gene several other approximations have been attempted. These have been based on the volume of the chromosomes, the number of genes known to to reside in the chromosomes, and the number of mutations that have been known to occur in a given chromosome; or on the number of mutations alone. As our knowledge of the number of genes increases, the maximum estimated size of the individual gene is necessarily reduced. Very recently the problem of gene action has begun to be attacked from the angle of the physical chemist by D. Wrinch (England) and other biochemists. It is thus shown that the giant protein molecules of which the chemists have built mental pictures through X-ray analysis and by other means come within the range of size postulated for the individual gene. At the present time no experimental evidence exists to prove the speculations that the gene in fact consists of a single molecule.

(3) East makes genetic analysis of partial sterility in tobacco hybrids.

1922—(1) Haploid *Datura* discovered by A. F. Blakeslee, J. Belling, M. E. Farnham, and A. D. Bergner (United States). This is the first discovery of a flowering plant developing with single instead of paired chromosomes.

(2) R. E. Cleland (United States) shows that characteristic arrangement of chromosome chains (rings) in *Oenothera* are typical of different species.

1923—(1) K. Sax (United States) demonstrates linkage between quantitative and qualitative characters in the garden bean.

(2) F. A. E. Crew (Great Britain) presents evidence to show that the "bulldog" calf, a nonliving monster frequently appearing in crosses of Dexter and Kerry cattle, is due to a lethal factor.

While other workers had suggested the inheritable nature of this defect, Crew was the first worker to suggest the possibility of its being

a lethal Mendelian character, the first lethal character identified as such in the livestock breeds. Since that time many other lethals have been recorded. C. Wriedt (Norway) has noted a tendency for outstanding dairy sires to transmit lethal factors, suggesting a linkage between such lethals and factors of economic value. They are thus a matter of some importance to the practical breeder. Their genetic interest is considerable because of the studies they have made possible in the developmental history of genes, from fertilization to adult organisms—the first of these being the study of L. C. Dunn and W. Landauer (United States) on the "creeper" fowl.

1924—(1) Blakeslee and Belling produce pure-line *Datura* by self-fertilization of a haploid.

(2) W. R. Taylor adapts smear technique to plant cytology, simplifying previous cumbersome methods and making possible the study of a much larger amount of material.

(3) Blakeslee, Belling, and Farnham explain certain *Datura* mutants as being plants with an extra chromosome. Blakeslee suggests the term "simple trisomic" for such forms in a classification of chromosomal types.

(4) W. T. Swingle and R. W. Nixon (United States) coin the term "metaxenia" to describe the effect of the pollen on maternal tissue outside the embryo. They confirm earlier observations, hitherto generally discredited, that date pollen has a profound effect on time of ripening and some other genetic characters.

1925—(1) T. H. Goodspeed and R. E. Clausen (United States) publish an analysis of their "artificial species", *Nicotiana digluta*, showing that this form (which arose as a fertile seedling from a normally sterile first-generation hybrid) contains a complete diploid set of chromosomes of each parent species of the original cross (*N. glutinosa* L.×*N. tabacum* L.). This amphidiploid ("double diploid") is self-fertile but is sterile with the parent species. This mechanism for the production of fertile polyploids by doubling the chromosome number of sterile first-generation hybrids has been found to be of rather wide occurrence in plants.

Primula kewensis W. Wats. was the first of the amphidiploids to be noted. It arose as a fertile branch of a sterile hybrid. The phenomenon remained an enigma until Goodspeed's and Clausen's publication. *Nicotiana digluta* explained the origin of a considerable number of such "artificial new species." Among forms recognized as amphidiploids on the basis of Clausen's and Goodspeed's work are Karpetchenko's *Raphano-Brassica*, C. A. Jorgensen's *Solanum luteonigrum*, wheat-agropyron hybrids of the Russian workers, etc. Other true-breeding interfertile forms, essentially new species, have been produced by chromosomal rearrangement in *Datura*.

(2) E. S. McFadden (United States) produces the two wheats, Hope and H–44, from a cross betwen Marquis wheat and Yaroslav Emmer. In the mature plant stage these wheats have been found to be nearly immune from almost all the physiological races of stem rust now known.

(3) J. A. Clark and E. R. Ausemus (United States) point out that the near-immune reaction in Hope wheat is a new character in common hard red spring wheat, inherited as a dominant character. The Hope and H–44 wheats have since become successfully and extensively used in further breeding for stem-rust control.

(4) East and A. J. Mangelsdorf (United States) offer a genetic interpretation of self-sterility in *Nicotiana* as due to rate-of-growth genes affecting the pollen tubes.

1926—(1) Belling advances the segmental interchange theory of chromosome evolution (exchange of segments between chromosomes that are not homologous).

(2) J. Percival (England) publishes explanation of polyploid origin of 14 and 21 chromosome wheats.

1927—(1) Artificial (X-ray) transmutation of the gene, Muller in *Drosophila* and L. J. Stadler in plants (United States).

The discovery made almost simultaneously by Muller and Stadler and Goodspeed that X-rays, and by F. B. Hanson (United States) that radium produces abundant gene mutations is one of the great bonanzas of modern genetic research. In the short time since this discovery was made it has been shown that X-rays produce a variety of effects ranging from mutations in a single gene to profound rearrangements and reassortments of entire chromosomes. Since Muller's original announcement the radiation technique has been extended to other forms of wave energy. It is impossible to give in any detail the development in this very widespread and fertile field of research.

(2) T. S. Painter (United States) finds a chromosome deficiency in mice which, with associated genetic evidence, establishes the first case in mammals of locating a definite gene on a definite chromosome.

(3) J. H. Craigie (Canada) reports hybridization of rust fungi to produce new pysiological forms; reports mutation in rust fungi.

The discovery by Craigie that hybridization of rust fungi is possible has opened up a wide field of most interesting research in microgenetics. Other workers have shown that the disease-producing fungi that attack plants mutate rather frequently in respect to their ability to infect and affect a given strain. The problem of the plant breeder seeking resistance has been enormously increased in complexity by these discoveries, which necessitate methods of protection by breeding against an enemy whose physiological reactions change with no visible outward alteration.

(4) Belling, iron-aceto-carmine technique of chromosome staining, makes possible more detailed studies of chromosome structure.

(5) B. O. Dodge (United States) publishes first report on the genetics of *Ascomycetes* (fungi), which have some advantages for genetic research because their haploid nature makes direct observation of all gene effects possible. With this material C. L. Lindegren (United States) has recently produced the first chromosome map of genes in a lower plant.

1930—(1) Stadler finds that maize genes vary widely in rate of mutation (no mutation in 1½ million waxy gametes, 492 per million in red pericarp [*P*] gametes).

(2) H. A. Timofeeff-Ressovsky (Union of Soviet Socialist Republics) reports induced reverse gene variations in *Drosophila*, demonstrating that X-ray effects are not purely destructive.

1930–37—The perfecting of the gene-frequency technique for the analysis of human inheritance by F. Bernstein (Germany), L. Hogben, J. B. S. Haldane, and L. S. Penrose (England), A. S. Wiener and L. S. Snyder (United States) makes possible much greater precision in the use of pedigree data, when the samples are too small to allow statistical treatment by older methods.

1931—(1) B. McClintock and H. Creighton (United States) in maize, and C. Stern (Germany) in *Drosophila*, prove crossing-over cytologically.

(2) McClintock and others of the Cornell group relate maize linkage groups to specific chromosomes by use of trisomics (diploid plants with one extra chromosome).

(3) Cleland and Blakeslee unify *Oenothera* and *Datura* cyto-genetic observations through segmental interchange theory.

(4) Wright gives first comprehensive picture of evolution in Mendelian terms, with stress on the balance and interplay between selection intensity, mutation rates, inbreeding, isolation, and migration.

1932—(1) L. F. Randolph (United States) produces tetraploid maize by heat treatment.

(2) Th. Dobzhansky (United States), and Muller and Painter show that "chromosome map" distance and actual (cytological) distance do not coincide.

(3) Variegation in *Drosophila* shown to be dependent on chromatin not organized into chromosomes (heterochromatin) by J. W. Gowen and and E. H. Gay (United States).

(4) J. M. Rasmusson (Norway) formulates hypothesis of interaction of genes to interpret certain observations of quantative character inheritance.

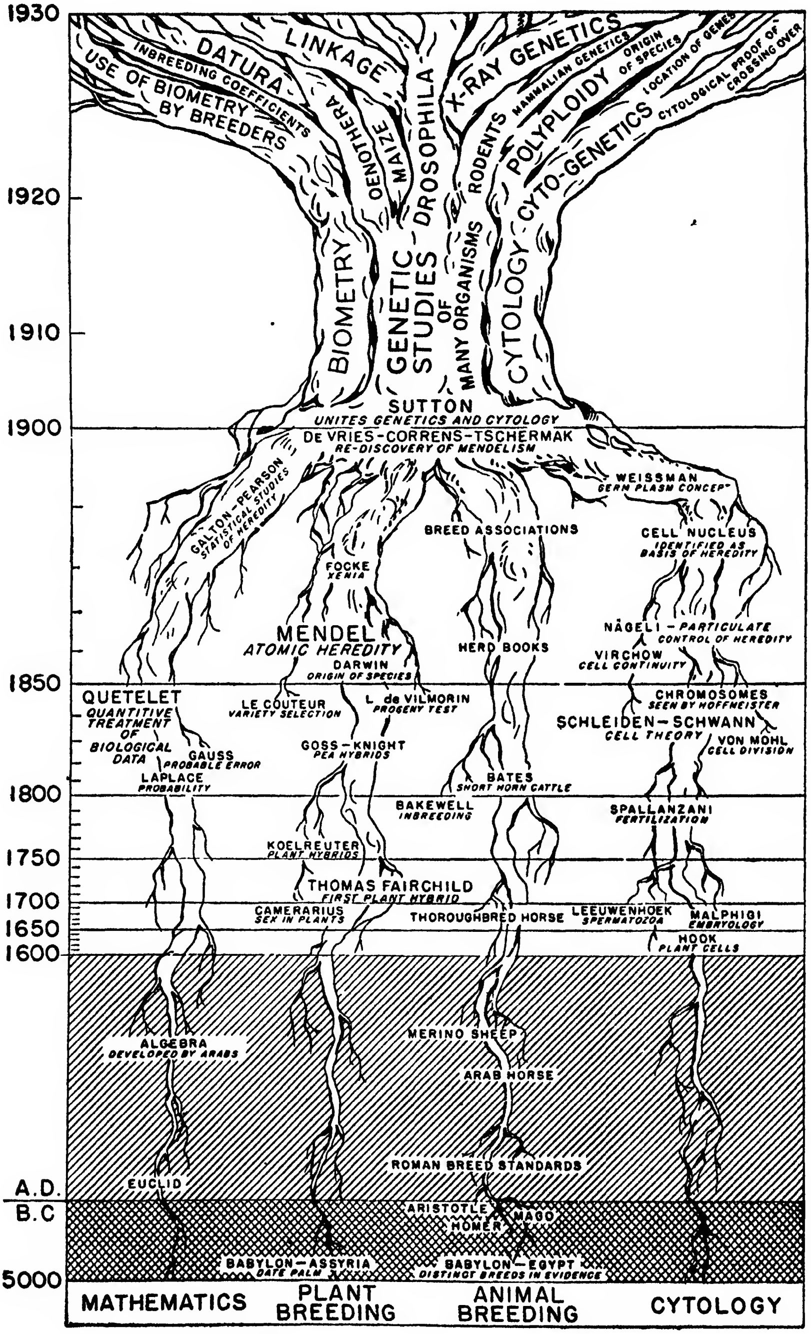
1934—Painter discovers genetic value of giant salivary gland chromosomes (discovered many years earlier, but considered a cytological curiosity), making possible detailed studies of chromosome structure, and leading to very exact location of genes.

THE FAMILY TREE OF GENETICS

It is customary to visualize historical development by analogy to a tree, whose roots go back into the distant past, whose trunk symbolizes a nicely unified development, and whose spreading branches denote the wide ramifications of our pet discipline at the moment we are considering it. Under any circumstances such an analogy is probably hazardous, and with some misgivings we shall symbolize genetics as a tree which has drawn its sustenance from four main roots.

These four taproots of modern genetics are: (1) The genetics root, leading back through Morgan, Bateson, De Vries, Mendel, Koelreuter, etc.: (2) the cytological root, tracing through Belling, McClung, Wilson, Sutton, Van Beneden, Leeuwenhoek, to Hooke, who first saw and named the cell; (3) the biometrical root, tracing through Wright, Fisher, Pearson, Galton, Laplace; and (4) the animal-breeding root, tracing through the stud and herd books, through the breed founders (such as Bakewell, the Collings, and Bates of a century ago) to Mago the Carthagenian, who is to be credited with compiling the first recorded score card—which is still used, with surprisingly little modification. Other "roots" could also be thought of.

It should be borne clearly in mind that these roots have generally been entirely distinct through much of their developmental history. No experimental connection existed between the observational work of the hybridizers and that of the microscopists until Sutton in 1902 confirmed Haeckel's prediction (1866) that the nucleus would prove to be the vehicle of heredity. The observed facts of Mendelian heredity fitted the cytologists' finding that meiosis and fertilization were a method for keeping the chromosome complement constant. The heretofore independent concepts were thus mutually confirmatory and together made a complete picture. Since that time it has been increasingly difficult to ignore cytology in studying strictly genetic phenomena. Without the cytologist's aid much genetic work would remain purely speculative. In the case of polyploidy, for instance, cytological counts of chromosome number and observation of chromosomal behavior at the reduction division have been of tremendous importance. Similarly the mathematical root developed entirely independently until Galton and Pearson bridged a gap that previously had been so wide that few students of the subjects involved would have admitted any close relationship.



The family tree of genetics.

What of future developments? The chronologer can do no better than quote one of the greatest geneticists, T. H. Morgan:

> I have been challenged recently to state on this occasion what seemed to be the most important problems for genetics in the immediate future. I have decided to try, although I realize only too well that my own selection may only serve to show to future generations how blind we are (or I have been, at least) to the significant events of our own time.
>
> First, then, the physical and physiological processes involved in the growth of genes and their duplication (or as we say their "division") are obviously phenomena on which the whole process of reproduction rests. The ability of the new genes to retain the property of duplication is the background of all genetic theory. Whether the solution will come from a frontal attack by cytologists, geneticists, and chemists, or by flank movements, is difficult to predict.
>
> Second: An interpretation in physical terms of the changes that take place during and after the conjugation of the chromosomes. This includes several separate but interdependent phenomena—the elongation of the threads, their union in pairs, crossing over, and the separation of the four strands. Here is a problem on the biological level, as we say, whose solution may be anticipated only by a combined attack of geneticists and cytologists.
>
> Third: The relation of genes to characters. This is the explicit realization of the implicit power of the genes, and includes the physiological action of the gene on the rest of the cell. This is the gap in our knowledge to which I referred already at some length.
>
> Fourth: The nature of the mutation process—perhaps I may say the chemico-physical changes involved when a gene changes to a new one. Emergent evolution, if you like, but as a scientific problem, not one of metaphysics.
>
> Fifth: The application of genetics to horticulture and to animal husbandry, especially in two essential respects—more intensive work on the physiological rather than the morphological aspects of inheritance; and the incorporation of genes from wild varieties into strains of domesticated types.
>
> Should you ask me how these discoveries are to be made, I should become vague and resort to generalities. I should then say: By industry, trusting to luck for new openings. By the intelligent use of working hypotheses (by this I mean a readiness to reject any such hypotheses unless critical evidence can be found for their support). By a search for favorable material, which is often more important than plodding along the well-trodden path hoping that something a little different may be found. And lastly, by not holding genetics congresses too often.

It is probable that we are even now witnessing the development of another major branch of the genetic tree—the biochemical branch. It has long been guessed that genes must be chemical in their action, and the molecular nature of the gene has more than once been suggested and speculated on. Studies of the analysis and synthesis of the sex hormones, of growth hormones and cancer-producing substances, and of the filterable viruses are bringing to light effects that closely resemble the action of genes. The next great important advance may be to link the gene with the newer biochemistry, which will make it necessary to revise our "genetic tree" and to add another important root tracing through Wilstetter, Mendeleeff, Dalton, and Lavoisier, to the alchemists of the Middle Ages!

Thus while specialization has been essential to promote the progress of science, it is distinctly a danger that too much specialization may endanger continued progress, if it prevents the formation of such fruitful graft-hybrids in ideas as those that have contributed so greatly to the progress of genetics. The geneticist and the breeder of the future must be intelligently cognizant of many fields of knowledge that are more and more impinging on their chosen specialty. Synthesis of these increasingly complicated factors seems essential if progress is to continue.

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